


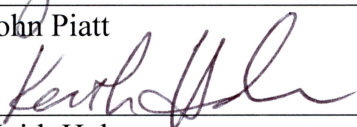
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IN THE GULF OF ALASKA

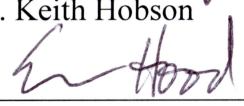
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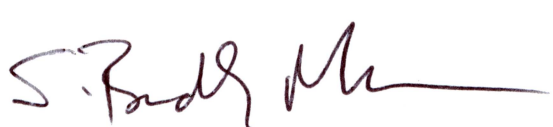

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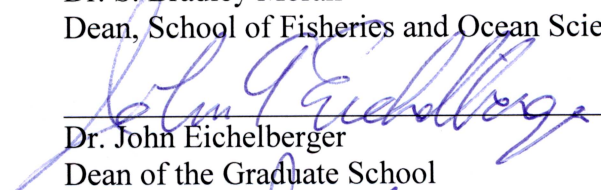

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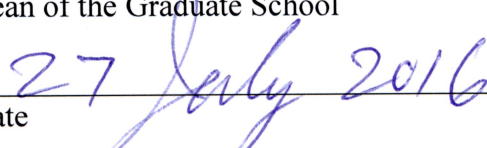

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THE INFLUENCE OF GLACIERS ON COASTAL MARINE ECOSYSTEMS
IN THE GULF OF ALASKA

A

DISSERTATION

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, AK

August 2016

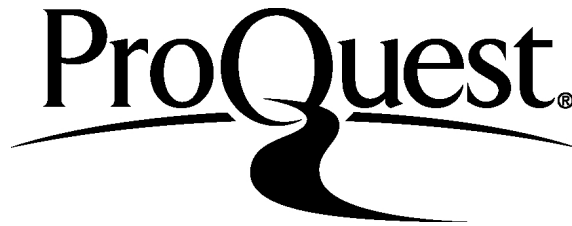
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Abstract

Glacier runoff (i.e., meltwater and rainwater discharged at the glacier terminus) provides about half of the freshwater discharge into coastal margins of the Gulf of Alaska, where contemporary glacier melting rates are among the highest in the world. Roughly 410 billion metric tons of glacier runoff enter the Gulf of Alaska each year. With freshwater discharge volumes of that magnitude, I hypothesized that glacier runoff has both direct and indirect effects on the receiving coastal marine ecosystems that support rich food webs, abundant and diverse marine communities, commercial fisheries and tourism industries. To examine the influence of glacier runoff on coastal marine ecosystems, I focused on three questions: 1) How does the marine food web respond to physical and biological gradients induced by glacier runoff? 2) What is the contribution of riverine organic matter (OM) and ancient carbon resources in glacier runoff to marine food webs from plankton to seabirds? and 3) How does the influence of glaciers on coastal marine ecosystems differ at small to large spatial and temporal scales? I measured physical, chemical and biological indices within four fjord systems along the eastern Gulf of Alaska coast. In chapter one I used geostatistics as well as parametric and non-parametric models to demonstrate a strong influence of glacier runoff on ocean conditions and coastal food webs across all the fjord systems. In chapter two I used isotopes ($\delta^2\text{H}$, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\Delta^{14}\text{C}$) to trace riverine OM and ancient carbon resources into the marine food web. This work included the development of a novel multi-trophic level 3-isotope Bayesian mixing model to estimate the proportion of allochthonous resources in animal tissues. Mean estimates from 14 species groups spanning copepods to seabirds ranged from 12 – 45 % riverine OM source assimilation in coastal fjords, but ancient carbon use by marine food webs was low. In the third chapter I synthesized information on the scale-dependent influence of glaciers on lower-trophic level productivity,

predator-prey interactions and ways that humans may be affected by anticipated changes in glacier coverage. This contemporary understanding of glacier influence on coastal ecosystems aligns with paleoenvironmental evidence suggesting that over geological time scales glaciers have and will continue to shape marine ecosystems in the Gulf of Alaska.

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Introduction

Alaska's glaciers comprise about 13 % of the world's mountain glaciers and they are among the largest continuous ice masses in high-latitude temperate ecosystems (Arendt et al. 2002). In the Gulf of Alaska (GOA) region, many of these glaciers terminate at or close to sea level, often in deep fjords created by glacial retreat. Alaska's glacial fjords provide important wintering, breeding, nursery and feeding areas for marine organisms, including top-level marine birds and mammals and commercially important fish and shellfish (Piatt & Gende 2007, Nielsen et al. 2007, Arimitsu et al. 2012). Rapid wastage of tidewater glaciers in coastal Alaska is contributing to rising global sea level and high rates of sedimentation from silty glacial river outflows (Larsen et al. 2015). Recent estimates suggest that 47 % of the annual freshwater discharge into the GOA originates from glaciers (Neal et al. 2010). This freshwater input, along with abundant rainfall and snowmelt, maintains the density gradient that drives the Alaska Coastal Current (ACC) and significantly influences marine productivity in nearshore regions of the GOA (Royer 2001).

Glacier runoff provides a link between terrestrial systems and nearshore coastal processes (Fellman et al. 2010), whereby freshwater input influences the physical oceanographic properties and circulation of fjords (Hill et al. 2009), and marine community structure is shaped by physical gradients in fjords (Renner et al. 2012). Although light limits primary production in the silty glacier plumes immediately adjacent to tidewater glaciers, the availability of inorganic nutrients in proximity to glacial streams (Gargett 1997, Smith et al. 2007, Piwosz et al. 2008, Vargas et al. 2011), and iron-rich freshwater discharge (Lippiatt et al. 2010, Schroth et al. 2011) or dust (Crusius et al. 2011) may be drivers of productivity at lower trophic levels. High and sustained chlorophyll a levels through the summer and fall have been observed in areas of intermediate

stratification, where glacier-influenced estuarine conditions meet more oceanic conditions in Glacier Bay (Etherington et al. 2007). Process studies provide multiple lines of evidence that zooplankton abundance is enhanced near glacier stream outflows (Weslawski et al. 2000, Robards et al. 2003, Arimitsu et al. 2012). Robards et al. (2003) suggested that seasonal zooplankton community dynamics in glacial areas of Glacier Bay were enhanced by local glacial runoff and oceanographic processes, as opposed to the lower bay, whose seasonal pattern was more consistent with general GOA trends. Arimitsu et al. (2012) attributed higher daytime near-surface euphausiid availability in proximity to glaciers to the lack of a photic cue for vertical migration in turbid waters. In glacial-marine systems, production at lower trophic levels translates to higher trophic levels as well. For example, forage species such as lanternfish (Myctophidae), and cold-water capelin are abundant in the near surface waters near glaciers (Abookire et al. 2002, Arimitsu et al. 2008). These areas are important foraging habitat for a variety of marine predators including some that are of management concern due to declining populations, such as Kittlitz's murrelets (*Brachyramphus brevirostris*) and harbor seals (*Phoca vitulina*) (Kuletz et al. 2003, 2011, Womble et al. 2010, Piatt et al. 2011).

Naturally occurring stable isotopes of some common elements can be used to trace the origin of those elements within marine organisms and upward through marine food webs (Michener & Schell 1994). This is especially true for carbon isotopes ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$), which are less prone to enrichment across trophic levels compared to nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) (Hobson et al. 2002). Carbon isotopic compositions are transferred relatively conservatively to biota from the diet, and are therefore useful tracers in food webs when dietary sources have large differences in $\delta^{13}\text{C}$ values, for example among oceanographically distinct marine regions (Schell et al. 1998, Kline, Jr. 1999), and between marine and terrestrial sources (Michener & Schell

1994). Likewise, Hood et al. (2009) found that $\delta^{13}\text{C}$ values in dissolved organic matter (DOM) from heavily glaciated watersheds were distinguishable from vascular plant-derived carbon. Therefore very different $\delta^{13}\text{C}$ signatures from inshore vs. offshore sources, terrestrial vs. marine sources, and also glacially-derived vs. non-glacially-derived sources can be expected. Additionally, hydrogen isotope ratios ($^2\text{H}/^1\text{H}$, $\delta^2\text{H}$) differ greatly between marine and freshwater sources. $\delta^2\text{H}$ in precipitation in Alaska is among the most deuterium depleted of all environmental waters (Hobson & Wassenaar 1997) and so there is a large ($>100\text{‰}$) potential gradient anticipated between hydrogen sources and biota. This suggests that $\delta^2\text{H}$ in addition to $\delta^{13}\text{C}$ measurements will allow the efficient tracing of terrestrial and marine organic matter and water sources in these systems.

Natural abundance radiocarbon (^{14}C) is a useful tool for tracing aged vs. contemporary organic matter through aquatic food webs. Glacial rivers draining glaciers have DOM that is old (4kyr ^{14}C -age) and more bioavailable to marine microorganisms compared to rivers dominated by a younger, plant-derived pool of DOM (Hood et al. 2009). Highly labile terrigenous DOM from glacial runoff can be an important source of carbon and nutrients to riverine and nearshore systems (Fellman et al. 2010, 2015). In the Chilean fjords riverine OM accounted for a significant percentage of copepod basal resources (20-50%) (Vargas et al. 2011). Taken together these findings suggest that ancient terrigenous carbon may be important to zooplankton, fish and seabirds in Alaska's glacial fjords.

The overarching goal of this work was to examine the influence of glacial runoff on the ecology of nearshore marine food webs in the Gulf of Alaska. This project built on an existing USGS research program to expand our understanding of community ecology and food webs in glacial ecosystems throughout the GOA. I collected new data in several fjords with glacial

influence to trace terrestrial and glacial isotopic signatures through nearshore marine food webs as part of a study funded by the North Pacific Research Board. In chapter one of my dissertation I used data collected in four fjords to compare and contrast the oceanography and prey distribution in seabird foraging areas that experience significant glacial influence. In chapter two I used an isotope approach to investigate the contribution of terrestrial-derived organic matter and ancient carbon to nearshore food webs. Finally, in chapter three I synthesized new (this study) and existing information on scale-dependent influence of glaciers on marine ecosystems in the Gulf of Alaska. Here I developed a conceptual graphic to communicate current knowledge of glacier influence on marine ecosystems.

Chapter 1: Glacier runoff strongly influences food webs in Gulf of Alaska fjords¹

1.1 Abstract

Melting tidewater and inland glaciers contribute a large volume of freshwater to coastal marine ecosystems in the Gulf of Alaska. The rate at which glaciers in Alaska are melting has increased markedly in recent decades, raising concern about ecosystem response to changes in freshwater discharge to coastal areas in the coming decades. To better understand the influence of glacier runoff on fjord ecosystems, we sampled oceanographic conditions, nutrients, zooplankton, forage fish, and seabirds within four fjords in coastal areas of the Gulf Alaska. We used generalized additive models and geostatistics to identify the range of glacier runoff influence into coastal waters within fjords of varying estuarine influence and topographic complexity. We also modeled the response of depth-integrated chlorophyll *a* concentration, copepod biomass, fish and seabird abundance to physical, nutrient and biotic predictor variables. Physical and nutrient signatures of glacial runoff extended 10-20 km into coastal fjords. Glacially modified physical gradients, nutrient availability, and among-fjord differences explained 66% of the variation in phytoplankton abundance, which is a driver of ecosystem structure at higher trophic levels. Copepod, krill, fish and seabird distribution and abundance were related to environmental gradients that could be traced to glacial freshwater input, particularly turbidity and temperature. Seabird density was predicted by prey availability and silica concentrations, which may be a proxy for upwelling areas where this nutrient is in excess. Similarities in ecosystem structure among fjords were due to influx of cold, fresh, and sediment laden water, while differences were likely due to fjord topography and region-specific estuarine

¹ Arimitsu, M., J. Piatt, and F. Mueter. 2015. Glacier runoff strongly influences food webs in Gulf of Alaska fjords. Submitted to Marine Ecology Progress Series.

vs. ocean influence. We anticipate continued changes in the volume and magnitude of glacial runoff will affect coastal marine food webs in the future.

1.2 Introduction

Glacial melt water provides a seasonal pulse of cold, sediment-laden freshwater to highly productive coastal areas of the Gulf of Alaska. Southern coastal Alaska has the largest system of temperate ice fields and glaciers in North America, nearly all of which are thinning and receding (Larsen et al. 2015). Rapid melting of coastal glaciers along the Gulf of Alaska is contributing to rising global sea level (Jacob et al. 2012) and has the potential to alter the physical, chemical and ecological properties of downstream freshwater and marine ecosystems (O’Neel et al. 2015). For example, freshwater runoff from glaciers (i.e., melt water, rain runoff, and ice calving) affects large-scale circulation and productivity in the region (Weingartner et al. 2005). Tidewater glaciers terminate at the sea in many of Alaska’s major fjords, which provide wintering, breeding, nursery and feeding habitat for marine predators of economic importance and conservation concern (Womble et al. 2010, Piatt et al. 2011, Nielsen et al. 2014). Understanding the factors affecting the ecosystem dynamics of the glacially-influenced region will help predict how continued climate warming will affect these important resources.

The delivery of glacial runoff and the resulting influence on physical oceanography is dependent on the glacier terminus position relative to submarine geomorphology (Motyka et al. 2003). Freshwater discharge may enter the ocean at depth below submerged glaciers causing localized upwelling and mixing near the glacier front and influencing downstream convection (Straneo et al. 2011, Bartholomaus et al. 2013). In contrast, discharge from glaciers that have grounded near or above the shoreline behaves like riverine discharge, which influences surface stratification and estuarine circulation (Stigebrandt 1981). Floating ice calved from glaciers also

brings cool fresh melt water into coastal marine waters, which is an important process where glacier mass loss from calving exceeds melting rates (Post et al. 2011).

Physical gradients caused by glacial runoff into the marine environment shape marine communities in fjords in Alaska (Renner et al. 2012) and Svalbard (Lydersen et al. 2014). Phytoplankton are limited by light availability due to high sediment loads near glaciers (Piwosz et al. 2008, Arimitsu et al. 2012). These pro-glacial systems still exhibit signs of higher trophic level production, including an abundance of copepods, krill and cold-water spawning forage fish (Arimitsu et al. 2008, Renner et al. 2012), seabird colonies and feeding aggregations (Mehlum & Gabrielsen 1993), and marine mammals that haul out on floating ice (Blundell et al. 2011).

The overarching goal of this work was to examine the influence of glacial runoff on the ecosystem structure across fjord ecosystems in the Gulf of Alaska. We sought to 1) describe the magnitude and range of influence of key physical characteristics associated with glacial runoff in coastal marine waters, and 2) characterize the distribution, abundance and response of lower to upper trophic level organisms relative to these glacially influenced gradients in a variety of marine physical parameters. We sampled oceanographic variables, nutrients, plankton, fish and seabirds at each of 172 stations within three study regions and four fjord systems in the Gulf of Alaska. We used geostatistical, parametric and nonparametric methods to assess the variability in environmental conditions relative to glacier runoff sources, and to characterize the response of chlorophyll *a* (chl_a), zooplankton, fish and seabirds relative to physical, chemical and biological indices in glacial fjords.

1.3 Methods

1.3.1 Study area

In order to understand marine ecosystem responses to fine-scale habitat gradients in coastal zones modified by glacial freshwater outflows, biophysical data were collected between 2004 and 2011 in three study regions that included four major glacial fjords systems around the Gulf of Alaska (Fig. 1). The fjord systems were chosen to represent a range of oceanographic conditions and fjord complexity within the glaciated region of the southern Alaska coast. College Fjord and Harriman Bay, sampled in 2010, are located in northern Prince William Sound (PWS), a large semi-enclosed embayment in south-central Alaska. Icy Bay and Yakutat Bay (IBYAK), both sampled in 2011, are located in southeast Alaska with direct oceanic influence from the Gulf of Alaska. In IBYAK, glacial melt water sources include the tidewater glaciers near the heads of the bays as well as glacial rivers entering nearshore areas adjacent to the Malaspina Icefield, a large piedmont glacier that separates the two bays. Glacier Bay (GLBA), sampled in 2004, is an estuarine fjord system with strong tidal influence due to topographic constrictions. Narrow fjords terminate in tidewater glaciers in the north and more oceanic influence is observed at its southern entrance. Each of 172 discrete stations within the three study regions was sampled once during the summer (June/July). This single “snapshot” approach made it impossible to assess annual variability, which may contribute to the regional differences we observed among study regions.

1.3.2 Data collection

In each fjord, sampling stations were chosen randomly from a 2.5 x 2.5 km grid overlaid on navigable waters in the fjord. The number of stations in each fjord was chosen to achieve a sampling frequency of about 1 sample per 15 km², and was based on available resources and

logistical constraints (weather, navigational hazards, vessel time). A suite of geographic, oceanographic, nutrient and biological attributes was sampled at each station (Table 1.1), details of which are given by Renner et al. (2012). Briefly, seabird densities were estimated at each station with a 300 m strip transect using standardized at-sea survey methods (Gould & Forsell 1989). Although we made efforts to avoid double counting animals during surveys, estimated bird densities are not comparable with other seabird censuses (e.g. Piatt et al. 2011) owing to the slow vessel speed while trawling (2-3 knots). During each 45 minute long marine bird transect, fish were sampled by towing a modified-herring midwater trawl with diminishing mesh size from 5 to 1 cm and approximately 50 m² mouth opening in near surface waters. The same net was used in all study regions to target near-surface waters (mean SE tow depth = 12 ± 1 m). Different research platforms (22 m F/V Steller in GLBA, 15 m R/V Alaskan Gyre at IBYAK and PWS), captains and deck gear were employed and this resulted in shallower mean depth of the headrope in GLBA (5 m) compared to IBYAK and PWS (20 and 21 m, respectively). Selectivity of this net is unknown but previous work showed that the net is effective at catching small (usually < 20 cm) schooling fish and euphausiids in a variety of coastal habitats (Speckman et al. 2005, Renner et al. 2012). Distance towed was estimated with a flowmeter (mean SE transect length = 2.78 ± 0.06 km). Zooplankton and oceanography measures were collected at the beginning or end of each transect. Zooplankton were sampled with a multinet (0.5 m² mouth opening with 505 µ mesh in GLBA) or a ring net (0.6 m diameter with 211 µ mesh in IBYAK and PWS stations) on a 50 m vertical haul or to within 5 m of the bottom in shallow water. Chla and inorganic nutrients were sampled with a water sampler near the surface and at 10 m depth (or at surface and 8 m in GLBA), and oceanographic conditions were sampled with a Seabird Electronics SBE25 (GLBA) or SBE19 (PWS and IBYAK) conductivity-temperature-depth

profiler (CTD) equipped with sensors to measure *in situ* temperature, salinity, chl_a, photosynthetically active radiation (PAR), and beam attenuation.

Trawl catches were weighed and total volume was measured in the field. Large catches were subsampled by volume. Fish were identified and enumerated by species, and the fork lengths of up to 50 individuals from each species were measured in the field. A subset of common fish (Table 1.2) were weighed in the lab to estimate forage fish biomass. Krill and gelatinous zooplankton total volume and wet weight were measured, but individuals were not identified to species. Zooplankton and trawl-caught larval fish that could not be identified in the field were preserved in 3-5% or 10% formalin, respectively. Water samples for inorganic nutrient concentration (μM) analysis were frozen in clean 60 ml HDPE sample bottles, and later processed at the University of Washington Marine Chemistry lab. Chl_a samples were processed by filtering 68 ml of sample water through GFF filters that were kept in dark conditions and frozen immediately. Acetone extraction and laboratory fluorometry of discrete depth chl_a samples for calibration of *in situ* fluorometer values are described in detail in Arimitsu et al. (2008).

Laboratory processing methods for zooplankton samples differed for each gear type. IBYAK and PWS ring net samples were identified to species and life stage whenever possible, up to 10 individuals per species/ life stage were weighed, and abundance was estimated using a plankton splitter after large organisms were counted and removed. After summing the weights by species and dividing by volume filtered, total zooplankton and copepod biomass (mg m^{-3} , IBYAK and PWS only) was calculated for each station at these study regions. These samples were processed at the University of Alaska Fairbanks. For GLBA multinet samples, bulk zooplankton samples were processed by estimating displacement volume to the nearest 0.25 ml,

converting displacement volume to relative wet mass assuming 800 mg cm^{-3} (Harris et al. 2000, p 140) and dividing by the volume filtered (m^3). The difference in sampling and processing methods preclude direct comparison of zooplankton biomass between GLBA and other study regions.

Dataset variables were summarized using selected study region-specific indices for descriptive and modeling purposes (Table 1.1). Geographic variables— including distance to land, distance to the nearest tidewater glacier, recently grounded glacier or major glacier river outflow (Fig. 1.1) and the total area of glaciers within 10 km of a station— were estimated using GIS. Distances were measured from each station’s transect midpoint. The current extent of glaciers was estimated by data provided by the Randolph Glacier Inventory (Arendt et al. 2014). Oceanographic variables were summarized by averaging the upper 5 m (near surface temperature, and near surface beam-attenuation, which is a proxy for water clarity, hereafter “turbidity”), 15 m (turbidity) and 50 m (temperature, salinity) of the water column. These depths were chosen to summarize the data because conditions from 0 – 5 m depths are most representative of the glacial freshwater signal (Etherington et al. 2007), while 15 or 50 m depth averaged conditions were most representative of the conditions experienced by the organisms we sampled. Photoc depth was estimated as the depth at which the PAR value reached 1% of the surface value. A stratification index was calculated as the average change per m in density ($\Delta\sigma\text{-t}$) within the upper 10 m of the water column (Etherington et al. 2007). Near surface nutrient concentrations were calculated as the average of concentrations at the surface and 8 (GLBA) or 10 (IBYAK and PWS) m depths. A nutrient index was calculated by scaling (mean = 0, SD = 1) and then summing dissolved inorganic nitrogen (DIN, sum of nitrate NO_3 , nitrite NO_2 and ammonium NH_4), silicic acid (SiOH_4) and phosphate (PO_4) concentrations.

Response variables for modeling variability at each trophic level were transformed to approximate normality and centered by subtracting the overall means. Calibrated fluorometer chl_a concentrations were integrated over the upper 15 m of the water column and fourth-root transformed. Copepod biomass data by species (Table 1.1) were summed to represent total copepod biomass at each station, and log-transformed. Gelatinous zooplankton volume, euphausiid volume and age fish abundance (excluding young of the year fish) was standardized by the length of the trawl tow in km. Seabird density was calculated by summing the number of pelagic-feeding marine birds (Table 1.2) sighted on the water within 150 m on either side of the vessel, and dividing by the area of the transect. Fish and seabird response indices were $\log(x + 1)$ – transformed prior to modeling. To model seabird density, we estimated prey availability using forage fish biomass in trawls, which was calculated by subtracting the biomass of adult pollock from the total fish catch weight. Adult pollock, the largest species in trawl catches, were excluded because they are generally too large to be targeted by foraging seabirds.

1.3.3 Data analysis

1.3.3.1 Range of melt water influence

Freshwater runoff creates variability in near surface fjord conditions, so we examined temperature (0-5 m), turbidity (0-5 m), stratification (< 10 m), and nutrients (< 10 m) to better understand the range of glacier melt water influence. We used generalized additive models (GAM) to evaluate the response of physical oceanography and nutrients in the surface waters in relation to the distance to nearest glacier runoff source (Fig. 1.1, Table 1.2). We used detrended ordinary krig geostatistical models to map near-surface conditions assuming second order stationarity and underlying spatial autocorrelation. Range, sill and nugget parameters for the spatial autocorrelation were estimated using weighted least squares regression implemented in

the ‘geoR’ package (Diggle & Ribeiro Jr. 2007) using R statistical software (v. 3.1.2, R Development Core Team 2014). When Euclidean distance was inappropriate for estimating pairwise distances due to the convoluted shorelines, we calculated pairwise distance through the water between points using the ‘gdistance’ package (van Etten 2015), and used principal coordinates analysis to create transformed coordinates that preserved these distances. A first order geospatial trend model with either Gaussian or exponential autocorrelation, depending on the variogram fit, was estimated via ordinary kriging. Predicted values were obtained at 1 km resolution within the maximum extent of the sample data, and back-transformed for mapping in GIS.

1.3.3.2 Chlorophyll *a*

Our *a priori* hypothesis was that phytoplankton abundance is related to nutrients, light and stratification. Because of strong multi-collinearity among the explanatory variables related to glacier melt water, including DIN, SiOH₄, PO₄, turbidity, temperature, and stratification, we conducted a principal component analysis (PCA) to obtain a reduced set of uncorrelated principal components (PCs) for modeling purposes. We explored ordinary least squares (OLS) models that included PCs and study region, and their interactions. Best-fit models were determined on the basis of minimum Akaike information criteria (AIC), and Moran’s I test for autocorrelation was used to assess whether residuals were independent. Where spatial autocorrelation was identified (Moran’s I $\alpha < 0.05$), generalized least squares (GLS) models were fit with an exponential correlation structure using transformed coordinates to preserve distance through the water (as above). GLS models were first fit using maximum likelihood estimation to allow comparison of AIC values among models. A likelihood ratio test (LRT) was then used to assess the overall significance of the model with the lowest AIC relative to the null model.

Finally, the AIC-best model was re-fit with restricted maximum likelihood (REML) for improved parameter estimates (Pinheiro & Bates 2000). The proportion of variance explained by the final GLS model was calculated as 1-variance of the residuals/variance of the response.

1.3.3.3 Zooplankton, Euphausiid, Fish and Seabirds

Our main objective was to fit a parsimonious model to describe the relationship between four response variables representing biomass, presence/absence or abundance of different trophic levels and the most influential predictor variables. Response variables for modeling included copepod biomass (PWS and IBYAK only), euphausiid presence/absence (0/1), fish abundance, and seabird density. Because of the large number of explanatory variables (Table 1.1), we used an exploratory approach to identify potentially important predictor variables and possible interactions for inclusion in modeling efforts. To identify predictors with the highest predictive accuracy we used boosted regression trees (BRT), a tree-based machine learning technique that applies a stochastic gradient boosting algorithm to improve predictive performance (Friedman 2001, Elith et al. 2008). BRT uses stochastic numerical optimization to minimize predictive deviance by fitting a large number of classification and regression trees to the data (De'ath 2007). The algorithm begins with a single tree, then weights each successive tree based on the incorrectly classified observations in the previous tree. The final classification is determined by optimized weighted majority of classifications and k-fold cross-validation (see details in Elith et al. 2008). We specified a Gaussian family in BRT modeling of copepod, fish and seabird responses. Due to the large number of zeros (66% of stations across study regions) in the euphausiid catch, however, we used a Bernoulli family on presence/absence data in the BRT analysis. We tested multiple parameter settings and found the models with lowest predictive deviance resulted when we set the learning rate to 0.001, bag fraction to 0.5, 5-fold cross

validation, and adjusted the tree complexity (from 1 to 5) for optimal prediction. The strength of first order interactions between predictors was quantified using functions provided in Elith et al. (2008) and the ‘gbm’ package (Ridgeway 2013). In addition to variables that represented prey indices (e.g., chl_a for copepods), and the categorical variable to account for study region (n = 3) or fjord differences (n = 4), predictors identified with high relative influence (generally > 10%) in the BRT analysis were used in OLS or GLS (when Moran’s I test indicated autocorrelation in OLS residuals at $\alpha < 0.05$) regression models using the same methods for model choice and diagnostics employed for the chl_a model. For euphausiid presence/absence data we used a GLM with binomial family and logit link. The performance of the AIC-best GLM model was evaluated on the basis of the proportion of fitted probabilities that resulted in correct classification of the response, where predicted probability ≥ 0.50 indicated presence.

1.4 Results

1.4.1 Range of melt water influence

Localized effects of glacier runoff could be traced 10-20 km into the marine system by a cooler near-surface signature, high turbidity and elevated nutrient concentrations (Figs 1.2-1.3). A non-linear fit to the nutrients and temperature indices at greater distances from the glacier was driven mainly by the presence of marine sills where mixing of cooler, nutrient rich deep water occurs in GLBA (the only site we sampled beyond 25 km from the nearest glacier runoff source, Fig. 1.1). Stratification was strongly influenced by complexity of fjord topography and bathymetry, whereby long, narrow fjords isolated by shallow marine sills (e.g., Harriman Fjord in PWS, Icy Bay in IBYAK, and Muir Inlet in GLBA) had greater stratification farther from glacier sources than fjords without sills (e.g., College Fjord in PWS and the west arm of GLBA), or areas with more direct oceanic influence (e.g., Yakutat Bay in IBYAK), (Fig. 1.3). Hubbard

Glacier, a tidewater glacier near the head of Yakutat Bay had less influence on stratification than runoff from the piedmont Malaspina Icefield draining into the Bay (Fig. 1.3).

The strength of glacier runoff effects on marine habitat in the four fjords was dependent on the degree of exposure to open ocean, the complexity of bathymetry and topography, and the type of glaciers present (i.e., tidewater vs. land-terminating). Near-surface nutrient concentrations were often greatest near glacial outflows, especially in the turbid tidewater glacial river plumes where nutrient demand by primary producers was low. In IBYAK higher nutrient concentrations were observed near Malaspina Icefield outflows and tidewater glaciers at the head of the Bays. In Yakutat Bay high nutrient concentrations were also sampled over shallow glacier-carved bottom features near the center of the Bay (Fig. 1.3). Likewise, in GLBA high nutrient concentrations were observed over the shallow marine sill at the entrance to the main bay likely as a result of tidal mixing of deep marine nutrients over a complex bathymetry and constricted passageway (Fig. 1.3, Etherington et al. 2007, Hill et al. 2009). Low N:Si ratios (Table 1.1) suggest silica is not limiting phytoplankton in glacial fjords (Gilpin et al. 2004), and average N:P ratios were below the Redfield ratio of 16:1 (Redfield 1958) suggesting nitrogen limitation particularly in PWS (Table 1.1). The highly stratified waters near the head of Muir Inlet differed markedly from the west arms of GLBA and fjord systems in other study regions. Most glaciers in this area are land-terminating except for one tidewater glacier that is separated from the inlet by a proglacial basin. Thirteen stations sampled closest to the head of Muir Inlet had above average chl_a concentrations that corresponded with lower N:P ratios (mean SE = 3.81 ± 0.53) and relatively elevated SiOH₄ (mean SE = $11.93 \pm 1.09 \mu\text{M}$). These findings are consistent with previous work that shows glacier runoff contains elevated levels of rock-derived elements such as silica and phosphate, and freshwater sources of nitrogen can be highest in moderately

glaciated watersheds dominated by early successional, nitrogen fixing vegetation (Hood & Scott 2008). Near tidewater glaciers in GLBA's western arm ($n = 12$), where subglacial melt water causes upwelling of deeper, nutrient rich waters, and at the shallow sill at the entrance ($n = 7$) had elevated levels of NO_3 (12.50 ± 0.84 and $12.80 \pm 1.25 \mu\text{M}$, respectively). Conditions there were more representative of nitrogen renewal from upwelled marine sources.

Study regions with less bathymetric and topographic complexity had lower spatial variation of near-surface ocean conditions compared to regions with greater complexity. For example, greater variability in temperature and nutrients was observed in IBYAK and GLBA over sills and narrow topographic constrictions compared to PWS (Fig. 1.3). The influence of runoff on turbidity was more strongly localized (< 10 km) than temperature or stratification (~ 20 km, Fig. 1.2) because sediment settles out but freshwater runoff from glaciers is buoyant.

1.4.2 Chlorophyll *a*

The first two principal components (PC) captured 80% of the variability in nutrients, turbidity, temperature and stratification. The different nutrients loaded similarly to one another along PC1 (0.44-0.48), while turbidity and temperature PC1 loadings had opposite signs to one another (0.39, -0.45, respectively). Stratification loaded strongly on PC2 (0.75). Residuals from an OLS regression of chl_a on PC1, PC2 and study region had significant spatial autocorrelation (Moran's I test, $p < 0.05$). The AIC-best GLS model (LRT: $p < 0.001$) accounted for an exponential correlation structure explained 66 % of the variability in chl_a using PC1 and study region as predictors (Fig. 1.4).

Chl_a concentrations were lower in PWS compared to other study regions (Table 1.3, Fig. 1.5), and a negative relationship with PC1 indicated decreasing chl_a concentration with increasing nutrients, higher turbidity and lower temperatures (Table 1.3).

1.4.3 Zooplankton

Zooplankton biomass in the upper 50 m of the water column was higher near glaciers at the head of fjords in estuarine study regions (GLBA and PWS), but lower near glaciers at the heads of fjords at the oceanic study region (IBYAK) (Fig. 1.5). In GLBA high zooplankton biomass was also observed over the sill at the entrance to the Bay, and in the shallow reaches of the eastern shore. We were unable to make direct comparisons of zooplankton biomass among sites (see methods). BRT analysis indicated ammonium and temperature were the best predictors of copepod biomass in PWS and IBYAK (Table 1.3). The AIC-best fit model included ammonium and an interaction between temperature and study region (OLS $R^2 = 0.27$, $p < 0.001$).

Copepod biomass was positively associated with temperature at IBYAK and negatively associated with temperature at PWS. In both study regions higher copepod biomass was coincident with higher ammonium concentrations.

1.4.4 Krill

Krill CPUE was highest in near-surface waters adjacent to glaciers (Fig.1.5). In IBYAK they also occurred near Malaspina Glacier outflows and marine sills in both Bays. They were generally absent at the shallow depths covered by the trawl away from glacier runoff sources, although their occurrence in deeper waters in the Gulf of Alaska has been well documented (Pinchuk et al. 2008). BRT analysis on presence/absence data indicated temperature, turbidity and gelatinous zooplankton had high relative influence on krill presence.

Krill occurrence in near-surface trawls was positively associated with high turbidity and low gelatinous zooplankton abundance. The interaction between the turbidity and gelatinous zooplankton was significantly different from zero (Table 1.3). This model predicted krill occurrence accurately in 77% of observations.

1.4.5 Fish

Fish abundance in trawl catches was high near tidewater glacier outflows, and near submerged sills that demarcate the previous position of glacier termini (Fig. 1.5). Large catches also occurred in areas of low turbidity away from glacial influence in Yakutat Bay and Glacier Bay. A simple index of proximity to glacial outflow, i.e., the proportion of total catch within 10 km of a glacier runoff source, revealed which species were more likely to occur in glacially modified habitats (Table 1.2).

For example, young-of-the-year fish, including walleye pollock, capelin and herring, dominated trawl catches (Table 1.2). Immature and spawning capelin, adult pollock and euphausiids were important in catches within 10 km of glaciers. In IBYAK and GLBA large catches of capelin were observed far from glaciers as well (Table 1.2). The typically mesopelagic northern lampfish was relatively abundant in shallow glacial waters in GLBA, and longfin smelt were observed only in IBYAK. Pacific sand lance were most abundant in areas without glacial influence in GLBA, which is consistent with their preference for relatively warm water areas in the Gulf of Alaska region (Robards 1999, Abookire & Piatt 2005). Gelatinous zooplankton volume was lowest in IBYAK, and the greatest proportion of the total catch was observed > 10 km from tidewater glaciers in all study regions (Table 1.2). BRT analysis indicated turbidity, gelatinous zooplankton and the interaction between these variables had a strong influence on fish abundance (Table 1.4).

Fish abundance was influenced by significant interaction between gelatinous zooplankton volume and turbidity. Due to limited overlap of these variables by site and the difficult interpretation of a three-way interaction, we ran separate regressions for each site. In PWS fish were more abundant in turbid waters with low gelatinous zooplankton catch, and lowest fish

catches occurred in clear water or where gelatinous zooplankton were more abundant (GLS, $R^2 = 0.48$, Table 1.2). The same relationship was observed in IBYAK (OLS, $R^2 = 0.43$, $p < 0.001$), and GLBA (OLS, $R^2 = 0.20$, $p < 0.001$).

1.4.6 Seabirds

The pelagic-feeding marine bird community was dominated by Black-legged Kittiwakes, Marbled and Kittlitz's Murrelets, and Glaucous-winged Gulls. Overall marine bird densities were highest in GLBA compared to other study regions (Table 1.1, Fig. 1.5). Seabird densities, especially those of murrelets, were probably underestimated in PWS and IBYAK because we sampled towards the end of the breeding cycle for many birds, and timing of breeding phenology may differ slightly among years (Arimitsu et al. 2011). BRT analysis revealed high relative influence of fish biomass, silica, temperature and fjord variables on seabird density (Table 1.4). Glacier distance was also important but was strongly correlated with other predictors so was not used in the regression analysis. We also explored models that contained interactions between silica, fjord and temperature as identified in the BRT analysis (not shown).

The most parsimonious seabird density model included silica, forage fish biomass, and temperature by fjord (GLS $R^2 = 0.43$, $p < 0.001$; Table 1.3). Higher density was observed with increasing silicic acid levels and increasing forage fish biomass. Higher seabird densities were associated with higher temperatures in YAK, but the slope of the linear relationship between seabird density and temperature was not significantly different from zero in GLBA, IB or PWS (Table 1.3).

1.5 Discussion

Similarities among the fjords we sampled could be traced to the unifying influence of glacial runoff during the summer melt season. Glacial runoff modifies near-surface gradients in

turbidity, temperature, stratification and nutrients in downstream coastal habitats up to 20 km away from glacier freshwater sources. Fine glacial sediment limits light within 10 km of glacier river sources, but a continual supply of riverine nutrients in runoff enhances phytoplankton where sediment settles out of the water column. The distribution of primary consumers and higher trophic level predators were influenced by glacially modified physical and chemical gradients in addition to biologically important variables like prey availability (Table 1.3). These findings add to previous work on oceanography and lower trophic levels (Burrell 1988, Gay & Vaughan 2001, Etherington et al. 2007, Piwosz et al. 2008), as well as higher trophic levels (Arimitsu et al. 2012, Lydersen et al. 2014, Grémillet et al. 2015) in glacially active coastal fjords.

Common in the surface waters across fjords was the high-turbidity, relatively elevated nutrient concentrations and low phytoplankton conditions in the glacial runoff plume. We also found similarities among study regions in the positive response of euphausiid occurrence and fish abundance to low gelatinous zooplankton and high turbidity conditions. Rich pelagic communities of euphausiids, spawning capelin, adult walleye pollock, snake pricklebacks, and stout eelblennies occurred in the dispersed marine scattering layer in the upper water column near tidewater glaciers. Seabird species well-adapted to turbid foraging conditions in the glacier plume, such as Kittlitz's Murrelets, Black-legged Kittiwakes and Arctic Terns were observed feeding on near-surface euphausiids upwelled during calving events and were also abundant in the glacial plume areas. Osmotic shock from freshwater may also cause euphausiid mortality near tide-water glaciers in these systems (Zajaczkowski & Legeżyńska 2001), creating easy prey for surface-oriented seabird predators.

Along with prey biomass, silica-rich glacial runoff was a structuring feature in seabird communities in the fjords we sampled. We observed a positive relationship between seabirds and forage fish biomass across all regions, which is not surprising given the high energetic demands of breeding marine birds (Cury et al. 2011). Less intuitively, our data indicated the inorganic nutrient silica was an important predictor of seabird density. Riverine sources provide roughly 80 % of the available silica to the world's oceans (Tréguer et al. 1995), and silica is an important component of the marine biogeochemical cycle particularly with regards to diatom formation (Pichevin et al. 2014). It's unlikely that the seabird-silica relationship was due to an indirect trophic linkage because the influence of chl *a* on marine bird density was relatively low (Table 4). A more likely explanation is that chemical weathering of rock and riverine inputs supply high levels of dissolved silica such that silica is not a limiting nutrient for primary production in the fjords. The data suggest that high concentrations of silica in the near surface waters may serve as a proxy for upwelling or frontal regions, which are known to aggregate prey and attract predators (Ainley et al. 2005).

While similarities among fjords were due to gradients caused by glacial runoff, differences among study regions were likely due to topographic complexity (bathymetry, constricted fjord passageways) that modifies nutrient availability through tidal action. Nutrient availability is a factor regulating periodicity in bloom conditions in PWS (Childers et al. 2005) compared to prolonged bloom conditions through the summer months in GLBA (Etherington et al. 2007), which may explain differences in chl *a* standing stock observed among study regions. Remotely-sensed chl *a* data suggests south-central Alaska and offshore areas adjacent to PWS undergo two chl *a* peaks in spring and fall, with lower chl *a* standing stocks through June and July (Waite & Mueter 2013). In contrast, high and sustained chl *a* standing stocks from spring through

fall months has been documented in GLBA (Etherington et al. 2007). This phenomenon is likely due to in part to nutrient replenishment from freshwater sources, and to a larger extent, to upwelling over sills and through constricted passageways after the initial spring bloom period.

We observed opposing patterns of zooplankton distribution relative to glacier freshwater influence in protected vs. oceanic bays and fjords (Fig. 1.5). Zooplankton biomass was highest near glaciers at the head of fjords in the most protected study region (PWS), in areas far from glacier runoff in the study region most exposed to open ocean (YAK), and both near and far from glaciers in GLBA. Our models explain relatively little of the variability in copepod biomass, which is likely influenced by factors we did not measure such as subsurface advection into the fjords associated with estuarine circulation resulting from substantial freshwater flow (Burrell 1988). The negative relationship between copepod biomass and temperature in PWS, the study region with lowest mean salinity in the upper 50 m of the water column (Table 1.1), suggests advection towards the head of the fjord is an important factor in their relatively higher abundance there. Basedow (2004) found advective gain of neritic copepod species and stages into fjords is related to fjord topography and sill depth. High zooplankton biomass at both ends of the glacier-induced habitat gradients is suggestive of differing processes affecting plankton dynamics in freshwater vs. marine regions. This has been previously shown through differing zooplankton productivity cycles in glacial vs. non-glacial areas of GLBA (Robards et al. 2003).

In conclusion, through this comparative study of fjord ecosystems in the Gulf of Alaska we found that near-surface conditions resulting from glacial runoff underpinned coastal ecosystem structure. Phytoplankton is regulated by light and nutrient availability, and both of these factors are modified in coastal waters by influx of freshwater associated with high levels of glacier runoff. Glacially modified habitat gradients influenced the abundance and distribution of

higher trophic levels in these productive coastal ecosystems. The crossroads of freshwater and marine influence, as well as tidal interaction with complex fjord geometry, creates productive waters for pelagic communities. Coastal areas in the Gulf of Alaska are important nursery areas for fish, feeding and breeding areas for marine predators, and of importance to resource managers. Most of Alaska's glaciers are receding rapidly, and glacier volume loss in the region is expected to increase through the 21st century (Radic et al. 2014, Clarke et al. 2015). We anticipate that continuing changes in volume and timing of glacier runoff will alter the land-to-ocean fluxes of freshwater, sediment and nutrients to coastal ecosystems (O'Neel et al. 2015). Our results suggest that future changes in material fluxes from glaciers will affect near shore marine food webs by altering the physical and biogeochemical structure of fjord ecosystems.

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Table 1.1. Mean (SE) values for glacier ecosystem model variables (abbreviation, measure, units) by study region (Glacier Bay, GLBA; Icy Bay and Yakutat, IBYAK; Prince William Sound, PWS). Some IBYAK measures are separated by fjord, IB/YAK, and "-" indicates not sampled. Nutrient samples were collected at the surface and either 8 m (in GLBA) or 10 m (in IBYAK and PWS).

Variable		PWS (n ₂₀₁₀ = 31)	IBYAK (n ₂₀₁₁ = 54)	GLBA (n ₂₀₀₄ = 87)
Geographic	area of glacier within 10 km (km ²)	64.4 (10.54)	5.43 (1.52)	15.35 (2.89)
Geographic	distance to tidewater glacier (km)	12.87 (9.00)	13.63 (6.14)	15.73 (12.14)
Geographic	distance to land (km)	1.48 (0.17)	4.05 (0.39)	1.04 (0.1)
Geographic	bottom depth (m)	174.39 (19.67)	107.27 (7.71)	148.26 (10.22)
Oceanography	photoc depth (m)	12.61 (1.61)	14.59 (0.96)	10.05 (0.55)
Oceanography	stratification (Δ sigma-t, Kg m ⁻³)	0.46 (0.03)	0.59 (0.04)	0.9 (0.05)
Oceanography	turbidity, beam attenuation in upper 15 m (m ⁻¹)	2.54 (0.44)	3.77 (0.63)	3.74 (0.45)
Oceanography	mean temperature in upper 50 m (°C)	8.20 (0.28)	7.76 (0.26)	7.41 (0.12)
Oceanography	mean salinity in upper 50 m	25.32 (0.14)	28.42 (0.17)	28.00 (0.14)
Nutrient	NH ₄ , mean of surface and 8 or 10 m ammonium concentration (uM)	1.09 (0.17)	1.13 (0.14)	1.53 (0.09)
	NO ₂ , mean of surface and 8 or 10 m nitrite concentration (uM)	0.07 (0.01)	0.13 (0.02)	0.24 (0.03)
	NO ₃ , mean of surface and 8 or 10 m nitrate concentration (uM)	3.75 (0.36)	4.36 (0.5)	5.46 (0.53)
	PO ₄ , mean of surface and 8 or 10 m phosphate concentration (uM)	0.61 (0.05)	0.65 (0.07)	0.73 (0.05)
	SiOH ₄ , mean of surface and 8 or 10 m silicic acid concentration (uM)	9.91 (0.61)	14.5 (0.67)	15.99 (0.71)
	DIN, dissolved inorganic nitrogen (uM)	4.91 (0.46)	5.63 (0.51)	7.23 (0.56)
	DIN:SiOH ₄ ratio	0.45 (0.03)	0.35 (0.02)	0.42 (0.02)
	DIN:PO ₄ ratio	7.39 (0.45)	9.08 (0.59)	11.0 (0.87)
	depth integrated chlorophyll <i>a</i> 0 -15 m (mg m ⁻²)	13.74 (0.95)	65.2 (5.54)	82.62 (5.67)
	^a zooplankton biomass (mg m ⁻³)	444.38 (45.41)	512.12 (59.26)	1540.17 (127.37)

Table 1.1. Continued

Variable		PWS (n ₂₀₁₀ = 31)	IBYAK (n ₂₀₁₁ = 54)	GLBA (n ₂₀₀₄ = 87)
Biology	copepod biomass (mg m ⁻³)	297.13 (42.09)	374.90 (45.19)	-
Biology	euphausiid trawl volume (ml km towed ⁻¹)	318.71 (200.64)	64.8 (21.01)	170.9 (89.02)
Biology	gelatinous zooplankton volume (ml km towed ⁻¹)	2422.78 (624.02)	1520.32 (554.81)	2611.66 (555.26)
Biology	fish abundance (number km towed ⁻¹)	40 (13)	194 (72)	107 (55)
Biology	forage fish biomass (g km towed ⁻¹)	130.1 (35.0)	316.7 (145.2)/ 1003.4 (339.1)	801.1 (111.8)
Biology	piscivorous seabird density (number km ⁻²)	4.34 (0.82)	9.71 (1.91)	38.33 (8.66)

^aGLBA mesh size: 335 µ and displacement volume converted to biomass, IBYAK and PWS mesh size: 211 µ and biomass assessed directly

Table 1.2. Relative abundance of common taxa and their proportion in samples near glacier runoff sources in Gulf of Alaska glacial fjord systems (Glacier Bay, GLBA; Icy Bay and Yakutat, IBYAK; Prince William Sound, PWS) during summer. Abundance indices differed by taxa: copepods biomass (mg m⁻³); krill and gelatinous zooplankton volume (ml km towed⁻¹), fish abundance (km towed⁻¹), marine birds density (numbers km⁻²). "-" indicates not sampled, see methods. An asterisk indicates copepods were sampled at 85 sites.

Species	Mean Abundance Index (SE)				Proportion of total within 10 km of glacier runoff source			
	GLBA (n = 87)	IBYAK (n = 54)	PWS (n = 31)	All Sites (n = 172*)	GLBA (n = 36)	IBYAK (n = 16)	PWS (n = 13)	All Sites (n = 65)
<u>Copepod</u>								
Copepoda (all combined)	-	374.90 (45.17)	297.13 (42.09)	346.54 (32.65)	-	0.29	0.56	0.37
<i>Scolecithricella minor</i>	-	0.02 (0.01)	0.2 (0.2)	0.08 (0.07)	-	0.58	1	0.94
<i>Metridia okhotensis</i>	-	19.67 (5.79)	2.86 (1.76)	13.54 (3.82)	-	0.43	0.97	0.48
<i>Metridia pacifica</i>	-	1.04 (0.2)	6.26 (1.22)	2.94 (0.53)	-	0.32	0.68	0.6
<i>Microcalanus</i> spp.	-	0.2 (0.04)	0.08 (0.05)	0.16 (0.03)	-	0.45	0.64	0.49
<i>Pseudocalanus</i> spp.	-	260.71 (37.69)	165.02 (32.77)	225.81 (27.1)	-	0.29	0.58	0.37
<i>Calanus marshallae</i>	-	12.46 (1.64)	5.19 (1.82)	9.81 (1.29)	-	0.35	0.86	0.45
<i>Calanus pacificus</i>	-	0.02 (0.02)	0.02 (0.02)	0.02 (0.01)	-	0	0.71	0.34
<i>Neocalanus flemingeri</i>	-	0.46 (0.14)	0.02 (0.02)	0.3 (0.09)	-	0.47	1	0.49
<i>Neocalanus plumchrus</i>	-	0.19 (0.09)	0 (0)	0.12 (0.06)	-	0.63	0	0.63

Table 1.2 Continued

Species	Mean Abundance Index (SE)				Proportion of total within 10 km of glacier runoff source			
	GLBA (n = 87)	IBYAK (n = 54)	PWS (n = 31)	All Sites (n = 172*)	GLBA (n = 36)	IBYAK (n = 16)	PWS (n = 13)	All Sites (n = 65)
<i>Eucalanus bungii</i>	-	0.03 (0.03)	0.13 (0.05)	0.07 (0.03)	-	0.92	0.24	0.44
<i>Paraeuchaeta elongata</i>	-	0.01 (0.01)	0.06 (0.03)	0.03 (0.01)	-	1	0.77	0.81
<i>Centropages abdominalis</i>	-	1.59 (0.49)	4.33 (3.86)	2.59 (1.44)	-	0.55	0.9	0.77
<i>Heterorhabdus tanneri</i>	-	0 (0)	0.01 (0.01)	0.01 (0.01)	-	0	0	0
<i>Epilabidocera amphitrites</i>	-	0.06 (0.05)	0.01 (0.01)	0.04 (0.03)	-	0.07	1	0.13
<i>Acartia clausi</i>	-	0.02 (0.02)	0 (0)	0.01 (0.01)	-	1	0	1
<i>Acartia longiremis</i>	-	69.16 (9.62)	98.54 (12.63)	79.88 (7.76)	-	0.18	0.5	0.32
<i>Tortanus discaudatus</i>	-	0.04 (0.02)	0 (0)	0.03 (0.02)	-	0.33	0	0.33
<i>Oncaea</i> sp.	-	2.42 (0.69)	0.49 (0.13)	1.71 (0.45)	-	0.64	0.84	0.66
<i>Microsetella</i> sp.	-	0.01 (0)	0 (0)	0 (0)	-	1	0	1
<i>Oithona similis</i>	-	6.25 (0.82)	13.33 (0.99)	8.84 (0.73)	-	0.34	0.47	0.41
<i>Oithona spinirostris</i>	-	0.06 (0.03)	0.11 (0.06)	0.08 (0.03)	-	0.55	0.16	0.36

Table 1.2 Continued

Species	Mean Abundance Index (SE)				Proportion of total within 10 km of glacier runoff source			
	GLBA (n = 87)	IBYAK (n = 54)	PWS (n = 31)	All Sites (n = 172*)	GLBA (n = 36)	IBYAK (n = 16)	PWS (n = 13)	All Sites (n = 65)
<u>Krill</u>								
Krill (Euphausiacea)	341.81 (178.04)	64.54 (21.05)	637.42 (401.27)	308.04 (115.87)	1	0.03	1	0.93
<u>Gelatinous Plankton</u>								
Ctenophora, Cnidaria, Salpida	5222 (1110.58)	1534.61 (562.55)	4733.33 (1211.34)	3976.26 (638.04)	0.15	0	0.2	0.14
<u>Fish</u>								
Pacific herring <i>Clupea pallasii</i>	0.82 (0.43)	0.26 (0.19)	0.57 (0.37)	0.6 (0.23)	0.04	0.05	1	0.21
Pacific herring (YOY) <i>Clupea pallasii</i>	20.26 (17.05)	4.1 (2.07)	0.52 (0.19)	11.63 (8.65)	0.01	0.14	0.59	0.03
Northern smoothtongue <i>Leuroglossus schmidtii</i>	1.2 (0.89)	0 (0)	0 (0)	0.61 (0.45)	1	0	0	1

Table 1.2 Continued

Species	Mean Abundance Index (SE)				Proportion of total within 10 km of glacier runoff source			
	GLBA (n = 87)	IBYAK (n = 54)	PWS (n = 31)	All Sites (n = 172*)	GLBA (n = 36)	IBYAK (n = 16)	PWS (n = 13)	All Sites (n = 65)
YOY Northern smoothtongue <i>Leuroglossus schmidtii</i>	0.52 (0.44)	0 (0)	2.32 (0.89)	0.68 (0.28)	1	0	0.18	0.5
Capelin <i>Mallotus villosus</i>	30.08 (8.22)	94.44 (37.01)	5.25 (2.02)	45.81 (12.55)	0.69	0.03	1	0.27
YOY Capelin <i>Mallotus villosus</i>	484.07 (114.41)	88.97 (24.97)	10.91 (4.41)	274.75 (60.48)	0.49	0.04	0.77	0.48
Eulachon <i>Thaleichthys pacificus</i>	0.42 (0.22)	36.02 (28.31)	1.85 (1.15)	11.85 (8.92)	0.99	0.02	1	0.06
Pink salmon <i>Oncorhynchus gorbuscha</i>	14.64 (3.15)	0 (0)	0 (0)	7.41 (1.68)	0.05	0	0	0.05
Longfin smelt <i>Spirinchus thaleichthys</i>	0 (0)	2.65 (1.5)	0 (0)	0.83 (0.48)	0	0.04	0	0.04
Northern lampfish <i>Stenobranchius leucopsarus</i>	10.25 (8.78)	0 (0)	0 (0)	5.19 (4.44)	1	0	0	1

Table 1.2 Continued

Species	Mean Abundance Index (SE)				Proportion of total within 10 km of glacier runoff source			
	GLBA (n = 87)	IBYAK (n = 54)	PWS (n = 31)	All Sites (n = 172*)	GLBA (n = 36)	IBYAK (n = 16)	PWS (n = 13)	All Sites (n = 65)
Walleye pollock <i>Gadus chalcogrammus</i>	1.18 (0.51)	13.82 (11.34)	17.13 (9.61)	8.02 (3.97)	0.99	0	1	0.46
YOY Walleye pollock <i>Gadus chalcogrammus</i>	357.02 (213.94)	23.72 (10.03)	46.29 (18.82)	196.38 (108.72)	0.39	0.1	0.28	0.58
Daubbed shanny <i>Lumpenus maculatus</i>	0.02 (0.02)	0.22 (0.2)	3.72 (1.3)	0.75 (0.26)	1	0.91	0.99	0.98
Snake prickleback <i>Lumpenus sagitta</i>	8.11 (6.13)	29.81 (12.22)	0.28 (0.16)	13.51 (4.98)	0.94	0.7	1	0.77
Stout eelblenny <i>Anisarchus medius</i>	2.53 (2.27)	11.49 (5.24)	7.56 (4.04)	6.25 (2.14)	1	0.45	1	0.68
Pacific sand lance <i>Ammodytes personatus</i>	34.38 (29.11)	0.01 (0.01)	0 (0)	17.4 (14.74)	0	0	0	0
Pacific sandfish <i>Trichodon</i>	0.02 (0.01)	0.72 (0.27)	0 (0)	0.23 (0.09)	0.4	0	0	0.01

Table 1.2 Continued

Species	Mean Abundance Index (SE)				Proportion of total within 10 km of glacier runoff source			
	GLBA (n = 87)	IBYAK (n = 54)	PWS (n = 31)	All Sites (n = 172*)	GLBA (n = 36)	IBYAK (n = 16)	PWS (n = 13)	All Sites (n = 65)
<u>Marine Bird</u>								
Common loon <i>Gavia immer</i>	0 (0)	0.01 (0.01)	0 (0)	0.01 (0)	0	0	0	0
Red-throated loon <i>Gavia stellata</i>	0.05 (0.04)	0 (0)	0 (0)	0.02 (0.02)	0.77	0	0	0.77
Pacific loon <i>Gavia pacifica</i>	0.08 (0.03)	0.02 (0.02)	0 (0)	0.05 (0.01)	0.67	0	1	0.67
Common merganser <i>Mergus merganser</i>	0.04 (0.03)	0 (0)	0 (0)	0.02 (0.02)	0.63	0	0	0.63
Red-breasted merganser <i>Mergus serrator</i>	0.04 (0.03)	0 (0)	0 (0)	0.02 (0.02)	0.78	0	0	0.78
Glaucous-winged gull <i>Larus glaucescens</i>	2.18 (0.75)	1.4 (0.27)	1.36 (0.25)	1.78 (0.39)	0.42	0.22	0.5	0.38
Herring gull <i>Larus argentatus</i>	0.03 (0.01)	0.05 (0.03)	0.03 (0.02)	0.03 (0.01)	0.22	0.13	0	0.16

Table 1.2 Continued

Species	Mean Abundance Index (SE)				Proportion of total within 10 km of glacier runoff source			
	GLBA (n = 87)	IBYAK (n = 54)	PWS (n = 31)	All Sites (n = 172*)	GLBA (n = 36)	IBYAK (n = 16)	PWS (n = 13)	All Sites (n = 65)
Mew gull <i>Larus canus</i>	0.24 (0.06)	0.07 (0.02)	0.12 (0.04)	0.17 (0.03)	0.68	0.4	0.69	0.63
Black-legged kittiwake <i>Rissa tridactyla</i>	12.42 (5.67)	1.53 (0.27)	0.83 (0.18)	6.91 (2.89)	0.23	0.24	0.45	0.24
Arctic tern <i>Sterna paradisaea</i>	1.25 (1.17)	0.39 (0.11)	0.01 (0.01)	0.76 (0.59)	0.96	0.22	1	0.85
Caspian tern <i>Hydroprogne caspia</i>	0 (0)	0.01 (0.01)	0 (0)	0 (0)	0	1	0	1
Bonaparte's gull <i>Chroicocephalus philadelphia</i>	0.08 (0.03)	0.01 (0.01)	0.01 (0.01)	0.04 (0.02)	0.11	0	1	0.14
Aleutian tern <i>Onychoprion aleuticus</i>	0 (0)	0.06 (0.02)	0 (0)	0.02 (0.01)	0	0	0	0
Common murre <i>Uria aalge</i>	0.03 (0.02)	0.05 (0.03)	0 (0)	0.03 (0.01)	0	0.29	0	0.14
Pigeon guillemot <i>Cephus columba</i>	0.71 (0.2)	0.07 (0.03)	0.02 (0.01)	0.38 (0.1)	0.72	0.55	1	0.72

Table 1.2 Continued

Species	Mean Abundance Index (SE)				Proportion of total within 10 km of glacier runoff source			
	GLBA (n = 87)	IBYAK (n = 54)	PWS (n = 31)	All Sites (n = 172*)	GLBA (n = 36)	IBYAK (n = 16)	PWS (n = 13)	All Sites (n = 65)
Marbled murrelet <i>Brachyramphus marmoratus</i>	16.03 (4.38)	4.65 (1.61)	0.98 (0.27)	9.74 (2.32)	0.05	0.05	0.81	0.11
Kittlitz's murrelet <i>Brachyramphus brevirostris</i>	4.83 (1.26)	0.98 (0.42)	0.69 (0.37)	2.88 (0.67)	0.44	0.65	1	0.47
Ancient murrelet <i>Synthliboramphus atiquus</i>	0.09 (0.05)	0.14 (0.05)	0 (0)	0.09 (0.03)	0	0.33	0	0.17
Tufted puffin <i>Fratercula cirrhata</i>	0.09 (0.03)	0 (0)	0 (0)	0.04 (0.01)	0.11	0	0	0.11
Pelagic cormorant <i>Phalacrocorax pelagicus</i>	0.06 (0.03)	0 (0)	0 (0)	0.03 (0.01)	0.16	0	0	0.16

Table 1.3. Summary of results from regressions (ordinary least squares, OLS, generalized least squares, GLS, or generalized linear model, GLM) of ecosystem components as a function of predictors sampled in glacier fjords in the Gulf of Alaska. Glacier Bay (GLBA), Icy Bay (IB) and Yakutat (YAK, or combined study region: IBYAK) and Prince William Sound (PWS).

Ecosystem Component	Model	Predictor	Coef.	SE	t-value	p-value
Chlorophyll <i>a</i> ($r^2 = 0.67$)	GLS	Principal Component 1	-0.154	0.017	-9.161	< 0.001
		Study region:IBYAK	-0.208	0.165	-1.263	0.208
		Study region:PWS	-1.200	0.193	-6.226	< 0.001
Copepod Biomass ($r^2 = 0.27$)	OLS	Temperature	0.394	0.091	4.317	<0.001
		Ammonium concentration	0.214	0.079	2.711	0.008
		Study region: PWS	3.766	1.109	3.396	0.001
		Temperature*PWS	-0.550	0.153	-3.606	0.001
Euphausiid presence/absence	GLM	Gelatinous Zooplankton (GZ)	-0.299	0.082	-3.667	< 0.001
		Turbidity	1.348	0.313	4.310	< 0.001
		GZ-Turbidity interaction	0.289	0.101	2.868	0.004
Fish CPUE PWS ($r^2 = 0.48$)	GLS	GZ	-0.458	0.228	-2.009	0.055
		Turbidity	1.881	0.502	3.748	<0.001
		GZ-Turbidity interaction	-0.664	0.237	-2.802	0.009
Fish CPUE IBYAK ($r^2 = 0.43$)	OLS	GZ	-0.327	0.084	-3.901	<0.001
		Turbidity	0.855	0.604	1.415	0.163
		GZ-Turbidity interaction	0.268	0.121	2.213	0.031
Fish CPUE GLBA ($r^2 = 0.17$)	OLS	GZ	-0.156	0.112	-1.397	0.166
		Turbidity	0.782	0.251	3.117	0.003
		GZ-Turbidity interaction	0.146	0.152	0.957	0.341
Seabird Density ($r^2 = 0.43$)	GLS	Silica	0.060	0.015	4.040	< 0.001
		Forage fish biomass	0.086	0.038	2.261	0.025
		Fjord-GLBA	-1.239	1.463	-0.847	0.398
		Fjord-IB	-0.990	1.679	-0.590	0.556
		Fjord-PWS	-0.541	1.409	-0.394	0.702
		Fjord-YAK	-6.630	1.296	-5.115	<0.001
		Temperature: GLBA	0.110	0.207	0.529	0.597
		Temperature: IB	-0.064	0.305	-0.211	0.833
		Temperature: PWS	-0.194	0.269	-0.720	0.473
		Temperature: YAK	0.644	0.262	2.462	0.015

Table 1.4. Boosted Regression Tree (BRT) results for lower (copepod), middle (krill, fish), and upper (marine bird) trophic level responses to physical and biological habitat variables. Prey indices, study region, variables with relative influence > 10 % (in bold), and interactions (indicated by asterisks) were used in parametric models (see Table 1.3).

	Copepod	Krill (0/1)	Fish	Marine Bird
Tree complexity	5	2	4	2
No. of trees	3550	2700	1700	5800
Model residual deviance	0.28	0.74	1.45	0.40
CV deviance (SE)	0.54 (0.06)	1.03 (0.07)	2.33 (0.23)	0.78 (0.11)
Training data correlation	0.81	0.76	0.78	0.85
Relative Influence of Variables				
Predictor Variable	Copepod	Krill (0/1)	Fish	Marine Bird
Study Region	0.21*	0	0.58	2.33
Fjord	0.46	0.18	0.45	12.47*
Chlorophyll a	6.35*	3.36	2.75	3.27
Ammonium	17.41*	3.89	3.3	4.66
Nitrite	5.54	2.7	6.41	3.4
Nitrate	5.8	4.24	3.31	3.65
Silica	7.17	5.23	5.09	12.15*
Phosphate	3.8	3.58	3.35	2.33
Temperature (ave. 50 m)	12.59*	16.6	4.5	11.29*
Salinity (ave. 50 m)	6.94	4.85	1.82	2.25
Turbidity Index (ave. 15 m)	5.4	22.6	25.89*	2.03
Stratification	5.07	1.06	2.98	4.06
Glacier area within 10 km	3.64	2.01	0.89	0.54
Bottom Depth	5.43	2.9	5.5	2.43
Distance from shore	2.75	1.37	3.06	3.87
Photic depth	2.86	6.12	1.46	1.35
Distance to glacier	3.7	4.15	4.18	9.6
Zooplankton biomass	-	1.93	2.76	2.98
Gelatinous zooplankton CPUE	-	11.78	14.89*	5.47
Krill CPUE	-	-	7.23	0.88
Forage Fish biomass	-	-	-	8.9

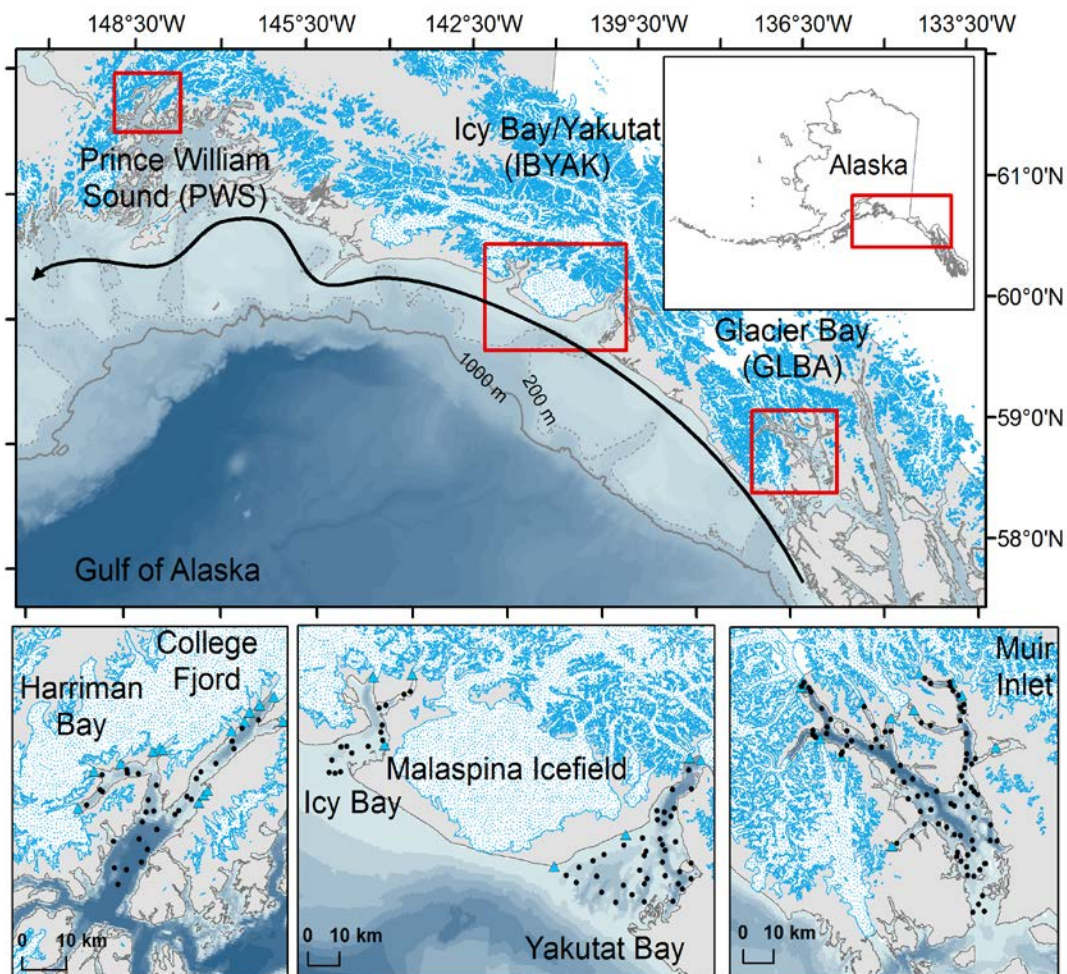


Fig. 1.1. Map of study locations with place names and site abbreviations, general coastal path of the Alaska Coastal Current (black arrow). Bathymetric contours are shown at 200 m (dashed) and 1000 m (solid), and relief shading indicates seafloor depth; (bottom) sample sites (black circles) and glacier runoff sources (blue triangles) in four fjords. Bathymetry and glacier coverage (blue stipple) courtesy of Lindquist et al. (2004) and Arendt et al. (2014), respectively.

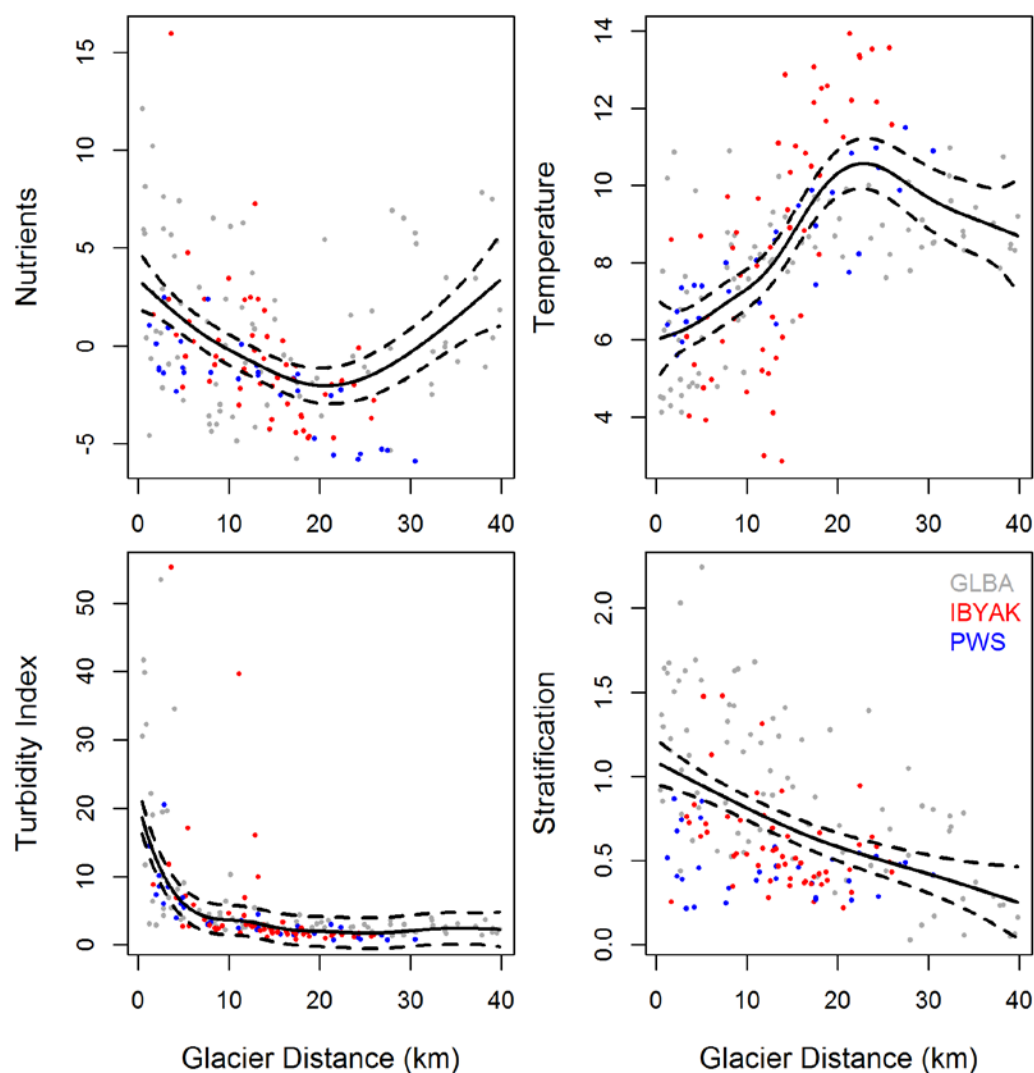


Fig. 1.2. Generalized additive model fits of physical and nutrient gradients relative to distance to nearest glacier runoff source (black line, ± 1 SE, dashed lines). Samples are shown as circles colored by study region, Glacier Bay (GLBA), Icy Bay and Yakutat (IBYAK) and Prince William Sound (PWS), Alaska. Nutrient index (μM , mean of 0 and 10 m samples) was calculated as the sum of scaled (mean = 0, SD 1) silica, dissolved inorganic nitrogen and phosphate. Temperature ($^{\circ}\text{C}$) and turbidity index (beam attenuation, m^{-1}) were averaged over the upper 5 m, and stratification ($\Delta\sigma\text{-t}$) was averaged over the upper 10 m of the water column.

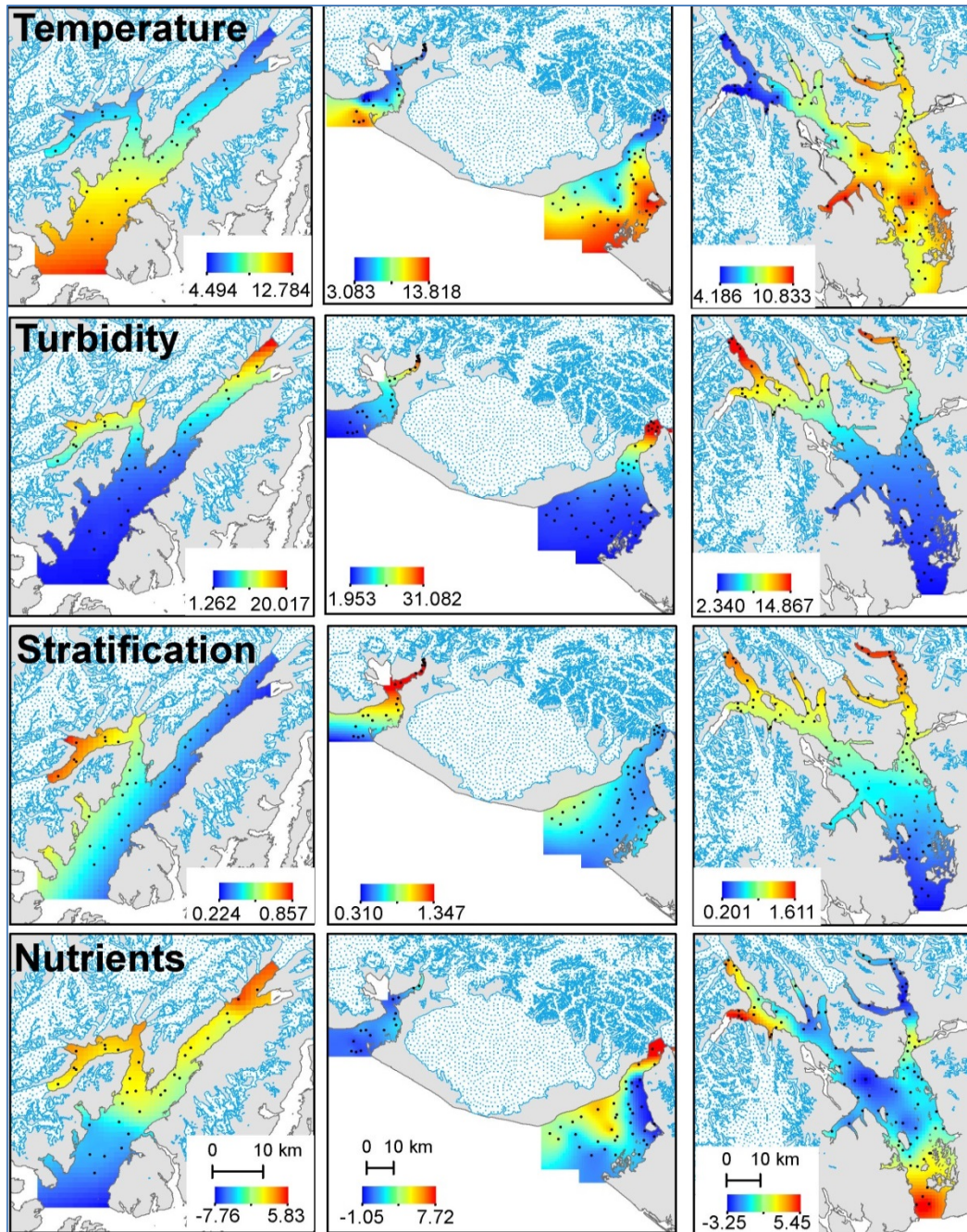


Fig. 1.3. Detrended ordinary krig models of temperature ($^{\circ}\text{C}$), turbidity index (beam attenuation, m^{-1}), stratification ($\Delta\sigma\text{-t}$), and nutrients index (sum of scaled nitrogen, phosphorous and silica, μM) in glacial fjords of the Gulf of Alaska during summer (left, Prince William Sound; middle, Icy Bay and Yakutat Bay; right, Glacier Bay). Note differing scales among study regions.

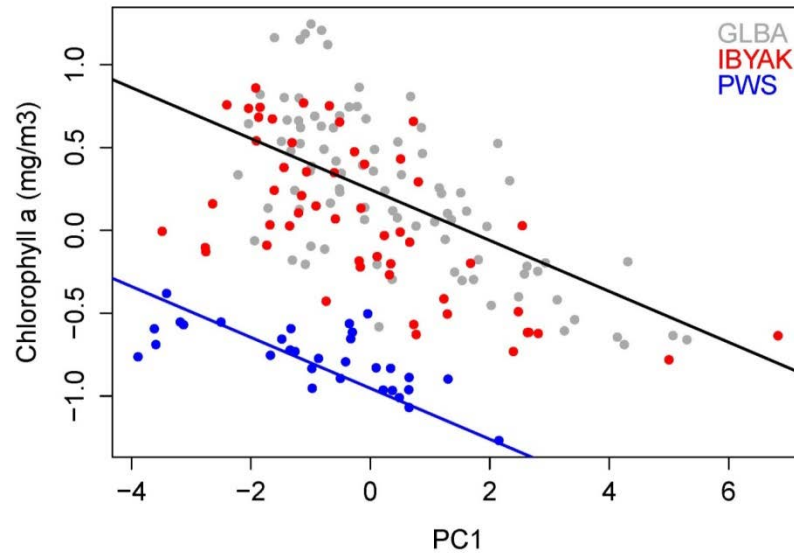


Fig. 1.4. Study region specific linear relationships between chlorophyll *a* concentration and the first principal component describing variability of glacially modified gradients in Gulf of Alaska coastal fjords (Glacier Bay, GLBA, Icy Bay and Yakutat Bay, IBYAK, Prince William Sound, PWS).

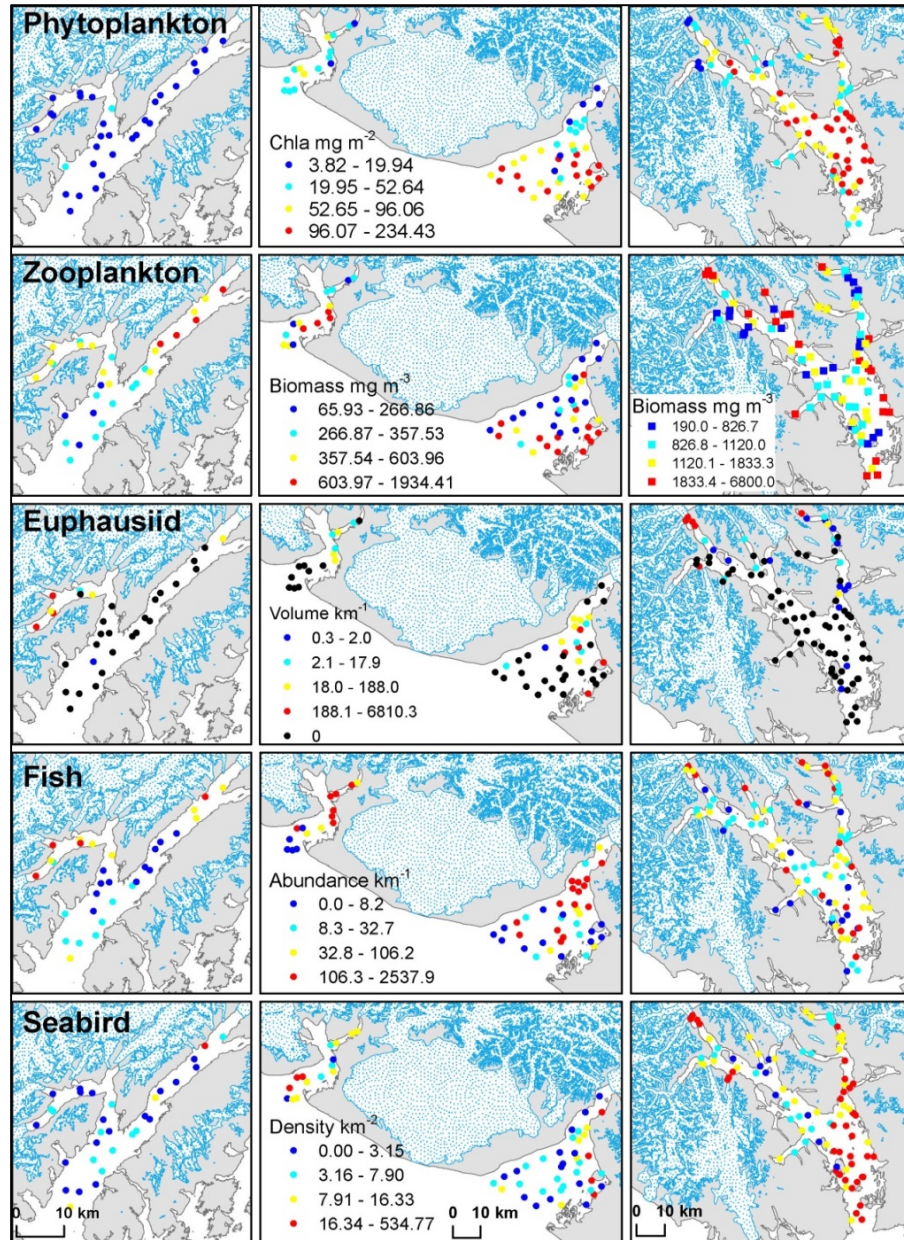


Fig. 1.5. Quantile map of trophic components measured in Prince William Sound (left), Icy Bay and Yakutat Bay (middle) and Glacier Bay (right), Alaska. Glacier ice is shown in blue stipple. Processing methods for zooplankton biomass in Glacier Bay (squares) differed from samples in other study regions (circles). Euphausiid volume and fish abundance in trawls was standardized by distance towed (km). Only pelagic-feeding (fish and zooplankton) marine birds sighted on the water were included in the seabird density index.

Chapter 2. Tracing biogeochemical subsidies from glacier runoff into Alaska coastal marine food webs*

2.1 Abstract

Each year 410 billion metric tons¹ of freshwater draining glacier landscapes in Alaska deliver riverine organic matter (OM) to coastal marine food webs that occupy the low phytoplankton turbid glacier plume waters, but the fate of this subsidy in marine food webs is unknown. Here we utilized large gradients in stable ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^2\text{H}$) and radiogenic ($\Delta^{14}\text{C}$) isotopes that trace riverine and marine OM sources as they are passed from lower to higher trophic levels in glacial-marine and oceanic habitats. Owing to carnivory rather than herbivory by krill, food chain length was greater in glacial-marine compared to oceanic habitats. Estimates of the riverine OM source contribution to upper trophic-level species including fish and seabirds ranged from 12 - 45 %, demonstrating that climate-driven changes in glacier runoff have the potential to alter food web dynamics in nearshore marine ecosystems along the Gulf of Alaska (GOA).

2.2 Introduction

Rates of glacier mass loss in Alaska over recent decades ($-75 \pm 11 \text{ Gt yr}^{-1}$ between 1994-2013) are among the highest on Earth and constitute a disproportionately high contribution to sea-level rise compared to other mountain glacier systems². Glacial runoff (liquid water and ice discharged at the glacier terminus) accounts for nearly half of all freshwater discharge into the GOA¹ and is a driver of the Alaska Coastal Current (ACC), a prominent circulation feature that can be traced from the N. Pacific into the Bering Sea and Arctic Ocean³. Glacier runoff from

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Alaska is projected to decrease 20% by the end of the century⁴ with important implications for the physical and biogeochemical properties of downstream marine ecosystems.

The trophic ecology of glacial-marine food webs is influenced by glacier-runoff driven habitat gradients^{5,6}. Within the turbid plume near tidewater glaciers, suspended glacial silt restricts light to the water column. Low light penetration into the water column not only limits phytoplankton biomass⁷ but also inhibits the vertical migration behavior of mesopelagic species (e.g. krill and dispersed plankton-feeding forage fish^{8,9}) that typically occur in deep (dark) water during light hours^{10,11}. The daytime occurrence of a shallow prey layer where glacier runoff enters the sea is a boon to surface-feeding seabird predators that exploit prey resources brought to the surface by calving events⁶, or those that are uniquely adapted to use these areas because of proximity to their glacial nesting habitat^{10,12}.

During peak melt season in summer, glacial-marine food webs may lack the high-quality autotrophic biomass needed to fuel them¹³. Allochthonous subsidies stabilize food webs where availability of local resources may be limited or variable in recipient habitats, for example when primary productivity in the recipient habitat is limited by availability of light^{14,15}. Although riverine systems typically have much lower levels of primary productivity than coastal marine systems¹⁶, riverine OM subsidies in glacial-marine food webs may be important because of low *in situ* primary productivity where light penetration is restricted by glacial silt.

The riverine OM carried in glacier runoff is a mixture of terrigenous OM from land plants, aquatic microbial OM and glacier-derived OM¹⁷, all of which are produced in environments dominated by ambient freshwater. As a result, glacier-derived riverine OM has a unique $^2\text{H}/^1\text{H}$ isotope ratio ($\delta^2\text{H}$) compared to OM derived from marine sources. Recent work on the processes underlying variation of $\delta^2\text{H}$ in food webs has facilitated the use of $\delta^2\text{H}$ as a

conservative tracer in food web mixing models^{18–22}. Thus the use of $\delta^2\text{H}$ in combination with more commonly employed stable isotopes for which gradients across freshwater and marine habitats ($\delta^{13}\text{C}$)^{23,24} and trophic discrimination ($\delta^{15}\text{N}$)²⁵ exist provides a framework for tracing the contribution of riverine OM in glacial-marine food webs.

In addition, the riverine OM draining glaciers is old (~2000–4000 years BP ^{14}C -age) compared to non-glacial riverine OM, which is dominated by younger, plant-derived material^{26,27}. This ancient carbon derived from glacier ecosystems can be readily assimilated into terrestrial^{28,29} and riverine food webs¹⁷, therefore we hypothesized that this ancient carbon subsidy may be an important resource to food webs at the glacial-marine interface.

Here we quantify the spatial extent and ecological impact of the flux of glacier-dominated riverine OM into glacier-marine habitats. We used $\delta^2\text{H}$ water isoscape mapping to assess the scale of mixing and infiltration of glacier runoff into coastal waters. We also evaluated differences in stable isotope and radiocarbon between food webs in glacial and oceanic habitats, and developed a novel Bayesian isotope mixing model to estimate the contribution of riverine OM to glacial-marine food webs.

Our study area was focused within Prince William Sound (PWS), an embayment approximately 8800 km² in area that is ringed by the heavily glaciated Chugach Mountain range in south-central Alaska (Fig. 2.1). We also contrasted isotope compositions among species in glacially modified marine habitats with their counterparts from truly marine habitats sampled in the western Aleutian Islands (see Methods), which are isolated from the freshwater signal of the ACC that flows northward through island passes to the east³⁰.

2.3 Results and Discussion

2.3.1 Glacier-marine hydrogen isoscape

The water hydrogen isoscape shows the lower $\delta^2\text{H}$ freshwater signal around the periphery of the embayment, and identifies cold fresh glacial runoff in the more heavily glaciated areas of the north and west fjords of PWS (Fig. 2.1). More saline ACC waters were distinct in near surface waters of the southern and central regions of the embayment despite interannual differences in temperature and salinity (i.e., 2.009 °C warmer and 0.786 PSU fresher at 10 m Hinchinbrook Entrance in 2013 compared to 2012), and this pattern is consistent with the dominant circulation of ACC waters through Hinchinbrook Entrance³¹. Cold fresh runoff from Columbia Glacier, the largest tidewater glacier in Alaska, can be identified in the hydrogen isoscape by lower water $\delta^2\text{H}$ values up to 45 km away from the glacier face (Fig. 2.1).

2.3.2 Glacier vs oceanic gradients in source and consumer isotopes

Glacier-dominated riverine, coastal and offshore sources were distinguished by their $\delta^{13}\text{C}$ and $\delta^2\text{H}$ values (Table S2.1 – S2.2). Measured coastal phytoplankton $\delta^{13}\text{C}$ values were distinct (range: -19.9 to -17.7 ‰), and although particulate OM $\delta^{13}\text{C}$ values overlapped in measured riverine (range: -26.3 to -22.5 ‰) and published offshore sources (range: -25.2 to -23.2 ‰)³², a strong gradient in $\delta^2\text{H}$ values between glacier-dominated riverine water (mean \pm SD -113.0 \pm 10.9 ‰) and marine water sources (mean \pm SD coastal -15.3 \pm 3.6 ‰, offshore -7.4 \pm 1.0 ‰) facilitated the use of these tracers in a mixing model. Riverine OM, coastal phytoplankton samples and published offshore OM values had overlapping $\delta^{15}\text{N}$ values, but riverine values were much more variable (mean \pm SD 4.4 \pm 3.9 ‰, 3.1 \pm 0.6 ‰, and 3.6 \pm 0.2 ‰, respectively).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of most biota sampled at the oceanic habitat were distinct from those in glacial-marine habitats (Table 2.1, Fig. 2.2). Bayesian estimation of the difference in

means analysis (BEST)³³ indicated intertidal mussels, representative of primary consumers, from glacial habitats were depleted in both ^{13}C and ^2H compared to oceanic habitats (BEST mean difference = -3.17 and -57.46 ‰, respectively). This pattern was likely due to greater availability of ^{13}C -enriched kelp-derived carbon³⁴, and ^2H -enriched seawater in the oceanic compared to the glacial habitat. High density credible intervals (HDI) of $\delta^{15}\text{N}$ values of mussels at both sites overlapped, indicating primary consumer $\delta^{15}\text{N}$ values were not different between glacial and oceanic habitats. For two species of fish, HDI of young of the year walleye pollock $\delta^{13}\text{C}$ values and sand lance $\delta^2\text{H}$ values overlapped between the two habitats. Otherwise, the pelagic food web in glacial habitats was ^{13}C -enriched and ^2H -depleted compared to oceanic habitats (Fig. 2.2). Mean $\delta^{15}\text{N}$ values of primary consumers (mussels, bulk zooplankton and copepods) were similar between glacial/coastal and oceanic habitats, but krill, fish and seabirds from glacial habitats had higher $\delta^{15}\text{N}$ values compared to their counterparts in oceanic habitats (Fig. 2.2, Table S2.3).

As the change in $\delta^{15}\text{N}$ values between higher predators relative to a common baseline is an indicator of food chain length³⁵, our data suggest the food chain was longer in glacial habitats compared to oceanic habitats. This difference occurred at the krill level and was transferred to planktivorous fish and piscivorous seabirds (Fig. 2.2). Krill appeared to be feeding on primary consumers (e.g., copepods) rather than phytoplankton in the light limited glacial-marine habitat. Thus omnivory by krill, which is known to vary by krill species and size distribution³⁶, is a key mechanism underlying the food chain length in glacial-marine habitats.

2.3.3 Ancient vs. modern carbon subsidies to glacial-marine food webs

Our findings suggest that the glacier-derived ancient carbon component of the riverine OM pool is not readily incorporated into food webs in glacier fjords, despite the fact that glacier OM can be highly bioavailable to marine heterotrophic organisms^{26,37}. The particulate OM in

glacial runoff and near surface coastal waters was depleted in ^{14}C (-780 to -176 ‰, 12100 to 1500 years BP ^{14}C -age). Likewise, dissolved organic carbon (DOC, -294 and 298 ‰; 2740 and 2780 years BP ^{14}C -age, respectively) in glacial runoff and near surface coastal waters and dissolved inorganic carbon (DIC) in glacial runoff (-272 ‰, 2770 years BP ^{14}C -age) were also depleted in ^{14}C . In contrast, DIC from coastal waters were enriched in ^{14}C (-22 to 70 ‰, 515 years BP to modern). Phytoplankton (-50 ‰, 440 years BP ^{14}C -age) and biota (-60 to 8 ‰, 530 years BP to modern ^{14}C -age) were also enriched in ^{14}C relative to riverine OM (Table 2.1). The fraction modern carbon in DOC and particulate OM was 0.71 (SD 0), and 0.55 (SD 0.2), respectively, but in phytoplankton, DIC and biota it ranged from 0.92 to 0.99 (Table 2.2). Furthermore, the fraction of modern carbon of biota in glacial-marine and oceanic habitats overlapped nearly completely (Table 2.2). These findings concur with previous work using isotopic tracers in the Arctic, whereby aged riverine-derived peat was available but not utilized by higher trophic organisms in the coastal marine system³⁸.

2.3.4 Riverine OM contribution to glacial-marine food webs

Riverine OM contributions to glacial-marine food webs varied by species as mean point estimates of posterior distributions ranged from 12 – 45% (Fig. 2.3). Source contribution estimates for relatively similar species showed marked differences. For example, despite their similar size, feeding habits and co-occurrence in GOA coastal waters, the glacier-nesting Kittlitz's murrelet rely on riverine OM sources to a greater extent than the congeneric marbled murrelet (43 % (SD 10%) vs. 17 % (SD 8 %), respectively). Marbled murrelets tend to be less associated with glacier ice¹⁰ and feed at a slightly higher trophic level than Kittlitz's murrelets³⁵. During the summer breeding season, Kittlitz's murrelets regularly feed on forage fish and krill within the turbid glacier plume because they are uniquely adapted to foraging conditions in close

proximity to their nests on or near tidewater glaciers^{10,39}. Marbled murrelets, on the other hand, obtain a lower proportion of their food resources from riverine OM sources by feeding throughout GOA coastal waters⁴⁰, although they are known to forage in freshwater lakes in some parts of their range⁴¹.

Likewise, two krill groups separated at the genus level appear to have different feeding histories; *Euphausia* tissues reflected greater use of offshore and coastal resources (54 % (SD 11 %) and 28 % (SD 10%), respectively) and *Thysanoessa* tissues reflected greater use of coastal and riverine OM resources (51 % (SD 10 %) and 36 % (SD 9 %), respectively). These patterns are consistent with the relative oceanic vs. neritic distribution (and thus, the feeding habits) of these species groups⁴². The relatively lower contribution of riverine OM sources to other macrozooplankton species, including the amphipod *Themisto* (14 % (SD 0.07%)), mysid *Neomysis* (12 % (SD 7%)) and krill *Euphausia* (18 % (SD 9%)) suggest lower residence time in this system than *Thysanoessa*. Feeding habits of these species, like other zooplankton, are likely related to advection and water mass characteristics^{43,44}. We note, however, that wide and overlapping 95% credible intervals for riverine and offshore marine OM sources for several species (Fig. 2.3) reflect a high level of uncertainty in estimates of source contributions, especially for plankton-feeding fish⁴⁵ such as young-of-the-year herring, eulachon, sand lance and walleye pollock, and the plankton and fish feeding⁴⁶ seabird black-legged kittiwakes.

2.3.5 Key findings and implications

Isotope compositions revealed a divergence in food web structure between glacial-marine and oceanic sites mediated by omnivory by krill. $\delta^{15}\text{N}$ values of krill suggest a feeding history of zooplankton at the glacial-marine site compared to a feeding history of phytoplankton at the oceanic site, and this difference was transferred up the food web. The longer food chain in the

glacial habitat may be due to reduced availability of marine phytoplankton resources because of low-light conditions in the turbid glacial plume waters. Despite the availability of labile ancient carbon from glacial runoff sources, radiocarbon signatures of higher trophic levels indicated modern carbon was more readily assimilated into the coastal marine food web. Still, species that regularly used the glacier plume habitat, such as krill (*Thysanoessa* spp.) and seabirds (Kittlitz's murrelet), were subsidized by riverine OM carried in glacier runoff during peak melt season. An important control on the variability in the assimilation of riverine OM subsidies among species is differential habitat use, or the amount of time spent foraging by a given species near glacier outflows during peak melt season. Given that stable isotope data suggest substantial contribution of terrigenous carbon to some species, we conclude the allochthonous subsidies to glacial-marine food webs were mainly in the form of young riverine OM sources released from glacier ecosystems and their surrounding watersheds.

The novel multi-trophic level Bayesian isotope mixing model presented here provides a new framework to evaluate trophic pathways and landscape connectivity in food webs. The large gradient in $\delta^2\text{H}$ isotopes in water and biota has been previously documented⁴⁷, however it is only recently that improved understanding in the discrimination factors that cause changes in ^2H abundance across trophic levels has allowed for the use of hydrogen isotopes in food web studies^{18,19,48}. Unique to our model is a multi-species approach which incorporated data across trophic levels to inform shared parameters on source and discrimination parameters while using far more data than would be feasible with a controlled laboratory study. Here we show this technique is a particularly effective tool for evaluating food web dynamics at the terrestrial-marine interface because of large gradients in ^2H between terrestrial (freshwater) and marine sources.

Climate warming is expected to result in earlier timing of peak discharge, flashy hydrographs, and greater interannual variability in freshwater delivery to coastal areas⁴⁹. As glaciers diminish in size discharge will decrease⁴, and watersheds will transition from glacial to non-glacial systems such that the delivery of terrigenous subsidies will become less regular and more event driven. Although a greater understanding of seasonal variability in subsidy use by species would inform predictions of trophodynamics relative to changing glacier coverage, we expect taxa with lower current use of allochthonous subsidies to be more capable of adapting to changing conditions. Changes to the timing and variability in magnitude and availability of allochthonous subsidies to coastal food webs may require coastal species to depend more on local resources. The effects of greater variability in the availability of allochthonous resources on species with substantial dependence on glacial subsidies will depend on their ability to exploit local resources. Virtually all of these species are capable of subsisting on marine resources, assuming they are available, however we anticipate ice-associated species like Kittlitz's murrelets in the GOA, who depend on glacier ice for nesting and are adapted to feeding conditions in the turbid glacier plumes, will be most negatively affected by changes in delivery and timing of glacial runoff to their coastal foraging habitat.

2.4 Methods

Methods and associated references are available in the supplementary information.

2.5 References

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2.7 Author contributions

M.A., J.P, K.H, E.H and J.F. designed the research, M.A, J.P, and K.H participated in field collections, K.H. processed stable isotope sample data, M.A. and D.W. analyzed the data, M.A. and D.W. prepared the manuscript with input from K.H., J.P., E.H. and J.F.

Table 2.1. Mean (SD) stable isotope composition and fish size (mean SD) of pelagic food web components sampled in July 2012 and 2013 in glacial-marine (Prince William Sound, Alaska) and oceanic (Aleutian Islands, Alaska) habitats. Due to size and life history differences, young of the year (YOY) fish are separated from age 1+ year classes. Lipids were extracted from all biota samples prior to analysis. Asterisks (*) indicates, for taxa with more than one sample at both sites, > 95% probability that mean difference in corresponding isotope values between sites is different from 0 using Bayesian estimation (BEST)³⁵.

Species (tissue, fish total length in mm)	n	Glacial-marine Habitat			n	Oceanic Habitat		
		$\delta^2\text{H}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$		$\delta^2\text{H}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Black-legged kittiwake (seabird liver)	28	-37.1	15.9	-18.3				
<i>Rissa tridactyla</i>		(11.2)	(0.5)	(0.5)				
Kittlitz's murrelet (seabird blood)	21	-106.6	14.7	-19.0	1	-91.3	10.4	-22.7
<i>Brachyramphus brevirostris</i>		(6.2)	(0.4)	(0.8)				
marbled murrelet (seabird blood)	18	-91.6	15.2	-18.6	4	-75.5	10.9	-22.7
<i>Brachyramphus marmoratus</i>		(6.5)*	(0.4)*	(0.4)*		(3.1)*	(0.9)*	(0.2)*
capelin (fish muscle, 96 ± 16)	43	-128.5	13.2	-19.0				
<i>Mallotus villosus</i>		(13.1)	(0.4)	(0.3)				
eulachon (fish muscle, 107 ± 34)	22	-158.6	14.8	-19.4				
<i>Thaleichthys pacificus</i>		(29.4)	(0.6)	(1.4)				
Pacific herring (fish muscle, 129 ± 33)	29	-118.2	13.5	-19.1				
<i>Clupea pallasii</i>		(11.5)	(0.5)	(0.4)				
walleye pollock (fish muscle, 275 ± 78)	40	-133.7	13.5	-18.6				
<i>Gadus chalcogrammus</i>		(11.9)	(0.8)	(0.6)				
Pacific sand lance (fish muscle, 106 ± 38)	26	-126.4	12.3	-19.4	7	-127.1	9.0	-22.6
<i>Ammodytes personatus</i>		(8.1)	(0.4)*	(0.6)*		(3.1)	(0.1)*	(0.3)*
YOY capelin (fish muscle, 32 ± 3)	12	-133.6	11.6	-19.9				
<i>Mallotus villosus</i>		(4.2)	(0.3)	(0.8)				
YOY Pacific herring (fish muscle, 35 ± 5)	40	-141.8	11.5	-20.3				
<i>Clupea pallasii</i>		(11.0)	(0.5)	(0.7)				
YOY walleye pollock (fish muscle, 49 ± 10)	42	-148.2	11.7	-19.5	6	-126.5	9.9	-20.6
<i>Gadus chalcogrammus</i>		(12.6)*	(0.6)*	(0.6)		(6.0)*	(0.7)*	(1.6)
<i>Euphausia pacifica</i> (krill, whole)	37	-135.8	11.0	-18.8				
		(14.3)	(1.2)	(0.5)				

Table 2.1. Continued

Species (tissue, fish total length in mm)	n	Glacial-marine Habitat			n	Oceanic Habitat		
		$\delta^2\text{H}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$		$\delta^2\text{H}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<i>Neomysis rayii</i> (mysid, whole)	16	-128.5 (5.5)	12.4 (0.5)	-18.4 (0.3)				
<i>Themisto libellula</i> (amphipod, whole)	15	-136.7 (4.6)	11.2 (0.5)	-18.0 (0.2)				
<i>Thysanoessa</i> spp. (krill, whole)	30	-157.1 (10.7)*	9.9 (0.6)*	-18.4 (0.8)*	6	-145.6 (2.4)*	7.9 (1.01)*	-20.8 (1.1)*
Bulk Zooplankton	6	-164.4 (8.1)	7.4 (1.2)	-19.8 (0.5)	1	-150.3	6.04	-22.2
Calanoid Copepod	4	-138.3 (8.5)	7.0 (1.4)	-20.2 (0.4)	1	-129.3	6.58	-22.12
<i>Mytilus trossulus</i> (mussel, muscle)	19	-152.8 (15.3)*	7.6 (0.8)	-19.1 (0.5)*	4	-95.2 (5.2)*	8.1 (0.5)	-15.9 (0.2)*
<i>Suberites</i> sp. (sponge, whole)	1	-86.1	7.24	-18.2				
Hairy triton	2	-87.1 (1.2)	12.0 (0.84)	-17.6 (0.1)				
<i>Fusitriton oregonensis</i> (snail, foot)	1	-66.5	13.9	-16.2				
Spot shrimp	1	-105.8	11.8	-15.7				
<i>Pandalus hypsinotus</i> (shrimp, whole)								

Table 2.2. Summary of radiocarbon data, including the mean (SD) fraction modern carbon, $\Delta^{14}\text{C}$ (‰) and radiocarbon age by sample type at a glacially-influenced coastal site (Prince William Sound) and an oceanic (Aleutian Islands) site in Alaska. Abbreviations: dissolved organic carbon, DOC; particulate organic matter, POM; dissolved inorganic carbon, DIC.

	n	<u>Glacial Habitat</u>			n	<u>Oceanic Habitat</u>		
		Fraction Modern	$\Delta^{14}\text{C}$	^{14}C Age		Fraction Modern	$\Delta^{14}\text{C}$	^{14}C Age
DOC	2	0.71 (0)	-296 (1)	2760 (28)				
			-455	5360				
POM (< 150 μ)	8	0.55 (0.2)	(196)	(3448)				
Phytoplankton	1	0.95	-50	440				
				720				
DIC	6	0.92 (0.11)	-38 (120)	(1022)*				
Mussel	1	0.94	-60	530	1	0.94	-53	525
Sponge	1	0.98	-10	130				
Snail	3	0.99 (0)	0 (3)	68 (33)				
Shrimp	1	0.99	3.00	65				
Copepod	1	0.97	-33	285	1	0.96	-44	345
Euphausiid	5	0.98 (0.02)	-15 (17)	170 (128)*	1	0.92	-79	650
Capelin	3	0.98 (0.02)	-18 (16)	187 (127)				
Eulachon	1	0.97	-27	285				
Pacific herring	1	0.97	-20	220				
Walleye pollock	1	0.95	-41	370				
Kittlitz's murrelet	3	0.99 (0)	-9 (6)	95 (33)	1	0.98	-25	180
Black-legged kittiwake	1	0.98	-12	145				

*modern samples were averaged as zero age

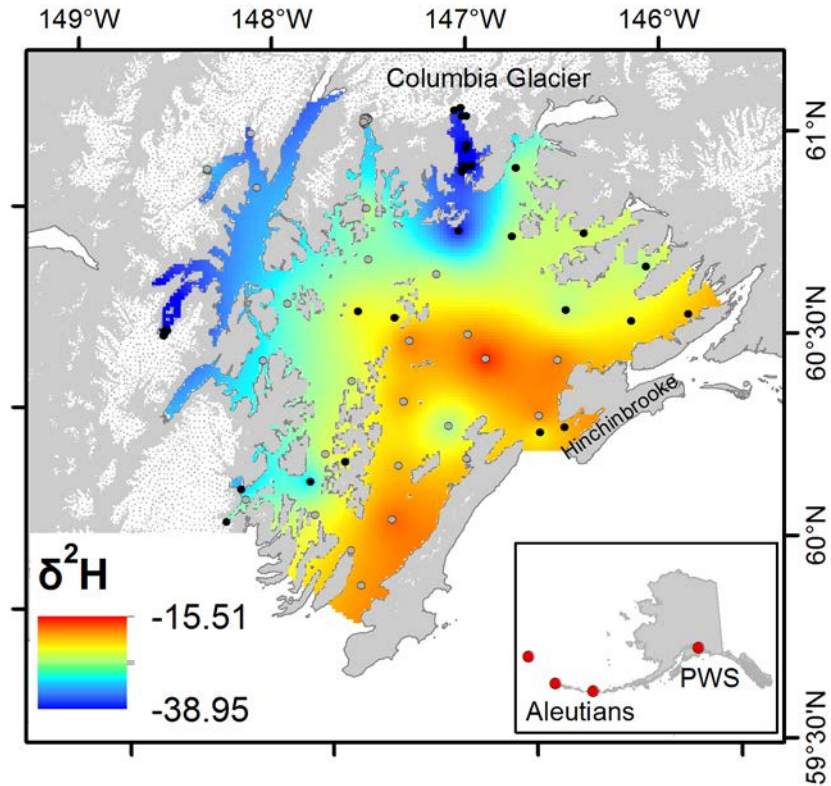


Figure 2.1. Map of the study area and hydrogen water isoscape (‰ VSMOW-SLAP) at 10 m depth in Prince William Sound (PWS), Alaska. Water sample locations are indicated by circles (grey = 2012, black = 2013), and color indicates krig predictions at 1 km² grid resolution. Inset: Oceanic (Aleutians) and glacial-marine (PWS) habitat sampling locations (red circles).

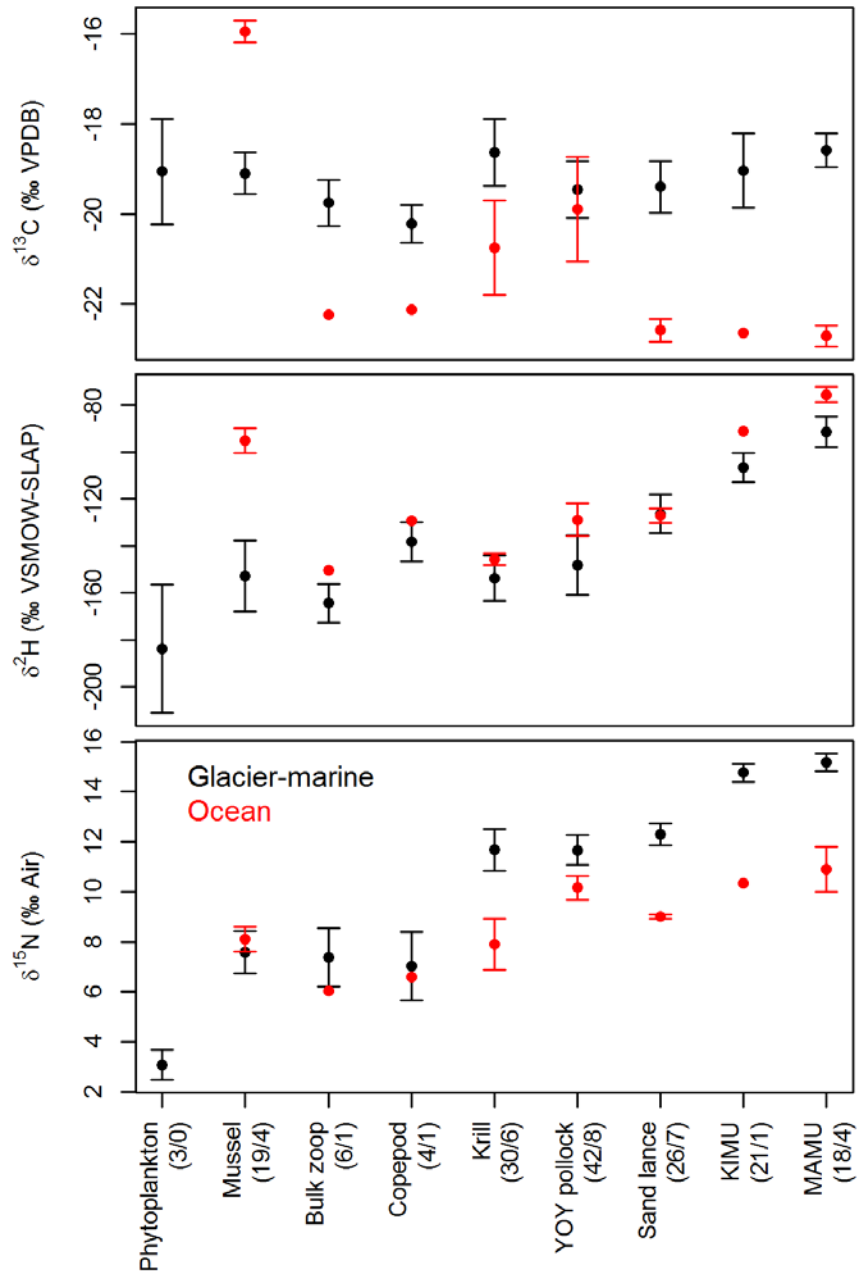


Fig. 2.2. Mean \pm SD of stable isotope ratios of biota sampled in glacial-marine (Prince William Sound, Alaska) and oceanic (Western Aleutian Islands, Alaska) habitats. Phytoplankton is shown for reference to other food web components, but was not sampled at the oceanic site. Sample sizes are given for each species (glacial-marine/oceanic). Other abbreviations: young of the year walleye pollock (YOY pollock), Kittlitz's murrelet (KIMU), marbled murrelet (MAMU).

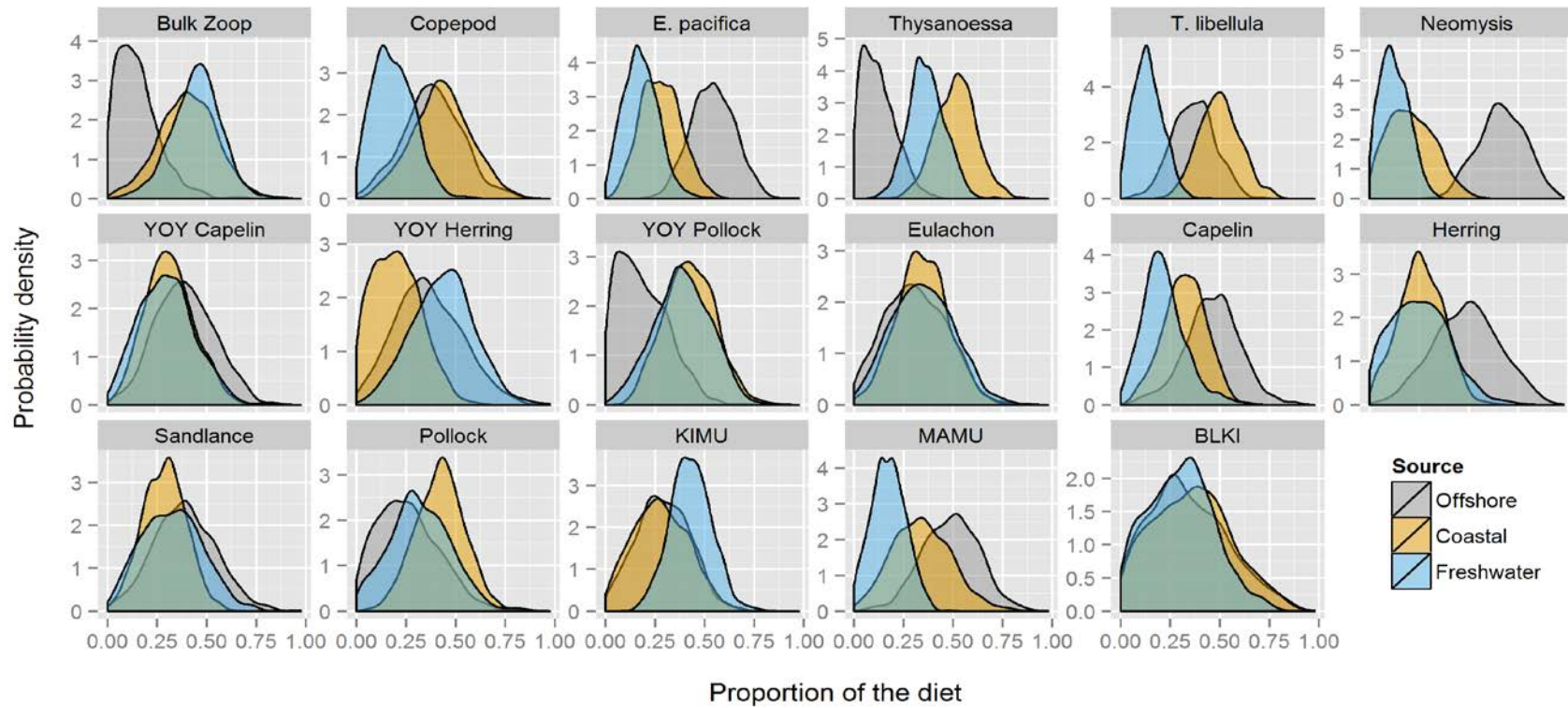


Fig. 2.3. Posterior density distributions of source organic matter contributions to species in a coastal marine food web with tidewater glacier influence. Abbreviations: young of the year (YOY), Kittlitz's murrelet (KIMU), marbled murrelet (MAMU), black-legged kittiwake (BLKI).

2.9 Appendices

Appendix 2.9.1 Supplemental information

2.9.1.1 Study area

Prince William Sound is an embayment approximately 8800 km² in area and ringed by the Chugach Mountain range in south-central Alaska (Fig. 2.1). Fjords with glacier influence are mainly located in the northern and western areas of the sound. The central region of the embayment is influenced by Gulf of Alaska (GOA) coastal waters, which enter through Hinchinbrook entrance, transit from east to west, and exit through Montague Entrance¹.

Our study sites in the Western Aleutian Islands were approximately 2500-3000 km from Prince William Sound, situated on a relatively broad, shallow shelf between the North Pacific and the Bering Sea. This site was chosen for its oceanic setting and isolation from influence of the Alaska Coastal Current which brings freshwater from the GOA to the Bering Sea through island passes to the east. Because sample collection in the Aleutians was conducted in conjunction with other work (John Piatt, USGS unpublished data), water and biota sample sizes were lower than at the glacial site.

2.9.1.2 Field collections

We collected water samples in Prince William Sound in 2012 and 2013, and at a single (marine) location near Attu Island (52° 50.807'N, 173° 28.056'E) in the Western Aleutians in 2013. Freshwater samples for $\delta^2\text{H}$ and $\delta^{18}\text{O}$ analysis were collected from melt water runoff near recently grounded glaciers, and seawater samples were collected from 2 and 10 m depths in 4-L Niskin bottles. We also collected a water sample near the bottom of each CTD cast, or to a maximum of 300 m depth (in 2013 only). These water samples were stored in tightly sealed 20 ml plastic vials with no headspace at room temperature until they could be processed in the lab.

Glacial runoff was collected in an acid-washed 4L container from streams on the beach adjacent to recently grounded glaciers in Blackstone Bay (60° 39.805'N, 148° 39.587'W), Columbia Bay (61° 7.614'N, 147° 1.781'W), and Icy Bay (60° 10.626'N, 148° 26.429'W). Seawater was collected in 4 L Niskin bottles using a Seabird Electronics SBE 19 plus v.2 conductivity-temperature-depth profiler equipped with an SBE55 auto-fire water sampler. Sample water was pre-filtered through a 150 μ mesh to remove zooplankton/detritus. POM was then filtered through a 47 mm glass fiber filter (0.7 micron) for stable isotopes or a pre-combusted (450°C for 4 hours) quartz filter (1.0 micron) for radiocarbon analysis ². Due to high sediment load, the total volume of water filtered through each filter was generally less than 1.8 L. Approximately 1 L of filtrate was stored in acid-washed polycarbonate bottles for ¹⁴C-dissolved organic carbon (DOC) analysis, and 250 ml of filtrate was stabilized with mercuric chloride and stored in a pre-combusted amber glass bottle (450 °C for 4 hours) with no headspace for DIC analysis ³. The POM filters and DOC samples were frozen in the field, and DIC samples were stored at room temperature until they could be processed in the lab. Water samples were also frozen in acid-washed 60 ml HDPE bottles for analysis of inorganic nutrients (nitrate, NO₃; nitrite, NO₂; phosphate, PO₄; silicic acid, SiOH₄; and ammonium, NH₄).

Representative biota from coastal food web components were sampled in marine waters with tidewater glacier influence. We also opportunistically collected biota samples at the oceanic Aleutian sites in coordination with a separate seabird diet study (Schoen et al. in prep). Thus, euphausiids and fish were collected in a different manner (see below) and sample size in the Aleutian sites is limited compared to Prince William Sound. Bulk plankton samples were collected with a 150 μ mesh ring net on a 50 m vertical haul and the net contents were placed in filtered water for 3 hours to evacuate any gut contents. After ~ 1 ml of bulk plankton was placed

in a vial, 20-40 large copepods were individually removed from the remaining bulk plankton sample and placed in a vial and frozen with ~1 ml of seawater. Copepods were identified to species in the lab; *Calanus marshallae* and *Neocalanus flemingeri* were the dominant large copepod species, while *Pseudocalanus* spp. and *Acartia longiremis* were the dominant small copepod in preserved samples. In Prince William Sound, euphausiids (*Euphausia pacifica*, and *Thysanoessa* spp. including a mix of *T. inermis*, *T. longipes*, *T. raschii*, *T. spinifera*), mysids (*Neomysis rayii*), amphipods (*Themisto libellula*), young of the year (YOY) fish (capelin, *Mallotus villosus*; Pacific herring, hereafter herring, *Clupea pallasii*; and walleye pollock, hereafter pollock, *Gadus chalcogrammus*), and age 1+ fish (capelin; herring; pollock; eulachon, *Thaleichthys pacificus*; and Pacific sand lance, hereafter sand lance, *Ammodytes personatus*) were collected with a modified herring trawl towed in the near surface water (< 20 m tow depth). Whole crustaceans were placed in a vial and frozen in the field. Fish dorsal muscle tissue was excised and placed in a vial and frozen in the field, or sometimes whole fish were frozen and muscle tissue was excised in the lab. In the Aleutian Islands, euphausiids (*Thysanoessa* spp., which were not identified to species), YOY and age 1+ fish were collected at seabird colonies from adults provisioning their chicks⁴. Mussels (*Mytilus trossulus*) were collected in the intertidal zone near glacier runoff in Prince William Sound, and near kelp and other intertidal organisms in the Aleutian Islands. Benthic organisms (marine sponge, *Suberites* sp.; snail, *Fusitriton oregonensis* and *Colus halli*, and spot shrimp, *Pandalus hypsinotus*) collected in a trawl near tidewater glaciers were frozen whole until they could be processed in the lab. Kittlitz's murrelets (*Brachyramphus brevirostris*) and marbled murrelets (*Brachyramphus marmoratus*) at coastal and oceanic sites were captured using the night lighting technique (Whitworth et al. 1997). Blood was drawn from the tarsal vein of murrelets and frozen in glass vials in the field.

Black-legged kittiwakes (*Rissa tridactyla*) were collected with a shot gun (Prince William Sound only). Black-legged kittiwake liver samples were frozen individually in glass vials. Replicate samples of a subset of biota from each taxon were placed in pre-combusted glass vials and frozen in the field for $\Delta^{14}\text{C}$ analysis.

2.9.1.3 Isotope analysis

POM filters were oven dried at 50 °C for 48 hours, and acidified with concentrated sulfurous acid to remove inorganic carbon. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses of POM were performed at UC Davis Stable Isotope Facility and within-run replicate of the laboratory standards had standard deviations of $< 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $< 0.2\text{‰}$ for $\delta^{15}\text{N}$.

Plankton ($> 150\text{ }\mu$) and other biota samples ($\delta^2\text{H}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$), as well as water samples ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) were processed at the Environment Canada lab, Saskatchewan. Samples were thawed, rinsed in distilled water, oven dried (plankton) or freeze dried (all other organisms) for 48 hours, powdered and treated with 2:1 chloroform methanol solution to account for variable lipid content across species and trophic levels. Crustaceans were soaked in 0.1 N HCl to remove carbonates. Stable carbon and stable nitrogen isotope assays were performed on 1 mg samples of homogenized materials by combustion at 850°C in a Robo-Prep elemental analyzer. CO_2 and N_2 gases were analyzed with an interfaced Europa 20:20 continuous flow isotope ratio mass spectrometer (Europa, ** USA) with every five unknowns separated by two (egg albumen) laboratory standards. Based on within-run replicate measurements of the lab standard, we estimated measurement error as $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$.

Water isotopes ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) were determined using off-axis integrated-cavity output laser spectroscopy (Model DLT-100; Los Gatos Research Inc.) using the method described in Lis et al. (2008). All samples were normalized to internal laboratory water standards previously

calibrated relative to VSMOW (0‰) and VSLAP ($\delta^2\text{H}$ -428 ‰ and $\delta^{18}\text{O}$ -55.5 ‰). Stable-hydrogen isotope analyses of organic materials were conducted using the comparative equilibration method⁶ through the use of calibrated keratin hydrogen-isotope reference materials (CBS: -197‰, SPK: -121.6‰, KHS: -54.1‰). The $\delta^2\text{H}$ isotope measurements were performed on H_2 derived from high-temperature (1350 °C) flash pyrolysis of 350 ± 10 ug tissue subsamples using continuous-flow isotope-ratio mass spectrometry (Isoprime, Manchester UK). Within-run (n=5) measurement of the three keratin laboratory reference materials (CFS, CHS, BWB) indicated measurement error < 2‰.

Natural abundance $\Delta^{14}\text{C}$ was analyzed for a subset of samples from each focal food web component at Woods Hole Oceanographic Institute by accelerator mass spectrometry using the methods of Raymond and Bauer (2001). Samples for analyses of $\Delta^{14}\text{C}$ in DOC, DIC, POM and biota were acidified with concentrated sulfurous acid to remove carbonates, combusted at 900 °C in double sealed quartz tubes, and the evolved CO_2 was purified and quantified on the vacuum extraction line⁸.

Isotope abundance is expressed in δ notation as the deviation from standards in parts per mil (‰) according to the following equation:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000 \quad (1)$$

where X is ^{13}C , ^{15}N , or ^2H , and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, or $^2\text{H}/^1\text{H}$. R_{standard} is based on Vienna PeeDee Belemnite (VPDB) for $\delta^{13}\text{C}$, atmospheric N_2 for $\delta^{15}\text{N}$, and Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation (VSMOW-SLAP) for $\delta^2\text{H}$.

Reported $\Delta^{14}\text{C}$ values were corrected for fractionation using the $\delta^{13}\text{C}$ values of the samples. Most samples had paired measures, however, $\delta^{13}\text{C}$ samples were lost in a small number of cases. We substituted the nearest within-fjord $\delta^{13}\text{C}$ value for two POM samples with missing

$\delta^{13}\text{C}$ values, and substituted the DIC $\delta^{13}\text{C}$ value of a sample with the most similar $\delta^2\text{H}$ water value for 3 missing DIC $\delta^{13}\text{C}$ measures. Because there was relatively little change in coastal marine DIC $\delta^{13}\text{C}$ (- 0.8 at 2 m depth, or 0.2 at 160 m depth) the difference in $\Delta^{14}\text{C}$ value when substituting one $\delta^{13}\text{C}$ value or the other was 2 ‰, and less than the range of expected error (5 – 10 ‰).

2.9.1.4 Isoscape modeling

We used geostatistics to graphically represent the extent of mixing and infiltration of cold, fresh glacier runoff into the coastal waters of Prince William Sound. We interpolated $\delta^2\text{H}$ values between water sample locations for 10 m depth using ordinary kriging with the ‘geoR’ package⁹. At both sample depths $\delta^2\text{H}$ values were linearly related to X and Y coordinates (OLS, $p < 0.001$ for 10 m depth), therefore we applied a first order trend and robust estimator when computing the sample variogram. We used an exponential covariance model and iteratively estimated the nugget, sill and range parameters first with weighted least squares (WLS) regression, and then with restricted maximum likelihood (REML) parameter estimation using the WLS parameters as initial values¹⁰. Krig predictions were made at a 1 km grid resolution within Prince William Sound.

2.9.1.5 Mixing model

We developed a Bayesian stable isotope mixing model to estimate basal source contributions, ϕ_{jl} to the pelagic food web in Prince William Sound. Let i be an individual, let j be a species (or species group), let k be a taxon specific tissue, and let l be a source (offshore, coastal, or freshwater). The trophic position for species j is

$$\tau_j = 2 + \frac{\delta^{15}\text{N}_j^{\text{obs}} - \delta^{15}\text{N}_{\text{base}}}{\Delta^{15}\text{N}_{jk}} \quad (2)$$

where $\delta^{15}N_j^{obs}$ is the mean of $\delta^{15}N$ values of observed consumer tissues for species j , $\delta^{15}N_{base}$ is the $\delta^{15}N$ values of baseline consumers (i.e., copepods in this nearshore pelagic system), and $\Delta^{15}N_{jk}$ is the per-trophic level discrimination factor for $\delta^{15}N$ by taxon-specific tissue for each species. The total trophic discrimination for ^{13}C and ^{15}N for species j , f_j^C and f_j^N , respectively, incorporate taxon specific tissue discrimination, $\Delta^{13}C_{jk}$ and $\Delta^{15}N_{jk}$, (here Δ notation represents the change in δX) of trophic levels below species j

$$f_j^C = \Delta^{13}C_{jk} \times (\tau_j - 1) \text{ and } f_j^N = \Delta^{15}N_{jk} \times (\tau_j - 1) \quad (3)$$

The expected $\delta^{13}C_j$ and $\delta^{15}N_j$ for species j is estimated to be a function of the $\delta^{13}C$ and $\delta^{15}N$ signatures of source l (s_l^C and s_l^N), the trophic discrimination for species j (f_j^C and f_j^N), and the proportion that species j feeds upon each source l (φ_{jl}), and we assume source contributions sum to 1

$$\delta^{13}C_j = \sum_{l=1}^3 \varphi_{jl}(s_l^C + f_j^C) \text{ and } \delta^{15}N_j = \sum_{l=1}^3 \varphi_{jl}(s_l^N + f_j^N) \text{ where } \sum_j \varphi_{jl} = 1 \quad \forall \quad (4)$$

The standard deviations of $\delta^{13}C_j$ and $\delta^{15}N_j$ (σ_j^C and σ_j^N) are a function of the variance of proportions of l sources for species j , φ_{jl}^2 , the standard deviation of each source ($\sigma_l^{s^C}$ and $\sigma_l^{s^N}$) and the standard deviation of total fractionation for species j ($\sigma_j^{f^C}$ and $\sigma_j^{f^N}$)

$$\sigma_j^C = \sqrt{\sum_{l=1}^3 \varphi_{jl}^2 \left((\sigma_l^{s^C})^2 + (\sigma_j^{f^C})^2 \right)} \text{ and } \sigma_j^N = \sqrt{\sum_{l=1}^3 \varphi_{jl}^2 \left((\sigma_l^{s^N})^2 + (\sigma_j^{f^N})^2 \right)} \quad (5)$$

The expectation and standard deviation of δ^2H differs from $\delta^{13}C$ and $\delta^{15}N$ because the δ^2H ratio in consumer tissues is influenced by δ^2H values of environmental water, $\delta^2H_j^w$ in addition to δ^2H signatures of dietary sources. There is a large photosynthetic fractionation (Δ^2H) between water and primary producers^{11–13}, but we assume no trophic discrimination at higher trophic levels^{14,15}.

For kittiwakes, we included an additional fractionation term, f_{BLKI}^H , to account for fractionation apparent in exploratory analyses of the data. Let ω_j be the proportion of $\delta^2\text{H}$ in consumer tissues due to water. The expected δ^2H_j is:

$$\delta^2H_j = \begin{cases} (\omega_j \times \delta^2H_j^w) + (1 - \omega_j) \sum_{k=1}^3 \varphi_{jl}(s_l^H + \Delta^2H) & \text{if } j \neq BLKI \\ f_{BLKI}^H + (\omega_{BLKI} \times \delta^2H_{BLKI}^w) + (1 - \omega_{BLKI}) \sum_{l=1}^3 \varphi_{jl}(s_l^H + \Delta^2H) & \text{if } j = BLKI \end{cases} \quad (6)$$

where $\sum_j \varphi_{jl} = 1 \quad \forall$

The standard deviation σ_j^H is a function of variance of proportions of l sources for species j , φ_{jl}^2 , the standard deviation of each source ($\sigma_l^{s^H}$) and the standard deviation of photosynthetic fractionation (σ^{Δ^2H}) and the standard deviation of the proportion of $\delta^2\text{H}$ due to environmental water (σ_j^ω). For kittiwakes we include an additional error term for fractionation, $\sigma^{f_{BLKI}^H}$

$$\sigma_j^H = \begin{cases} \sqrt{\sum_{l=1}^3 \varphi_{jl}^2 \left((\sigma_l^{s^H})^2 + (\sigma^{\Delta^2H})^2 + (\sigma_j^\omega)^2 \right)} & \text{if } j \neq BLKI \\ \sqrt{\sum_{l=1}^3 \varphi_{jl}^2 \left((\sigma_l^{s^H})^2 + (\sigma^{\Delta^2H})^2 + (\sigma_{BLKI}^\omega)^2 + (\sigma^{f_{BLKI}^H})^2 \right)} & \text{if } j = BLKI \end{cases} \quad (7)$$

For individual i of species j , $\delta^{13}C_{ij}^{obs}$, $\delta^{15}N_{ij}^{obs}$ and $\delta^2H_{ij}^{obs}$ in consumer tissues are assumed to be normally distributed about the expected value of each isotope for species j , $\delta^{13}C_j$, $\delta^{15}N_j$ and δ^2H_j with standard deviation σ_j^C , σ_j^N and σ_j^H

$$\delta^{13}C_{ij}^{obs} = \delta^{13}C_j + \varepsilon_i^C \text{ where } \varepsilon_i^C \sim N\left(0, (\sigma_j^C)^2\right) \quad (8)$$

$$\delta^{15}N_{ij}^{obs} = \delta^{15}N_j + \varepsilon_i^N \text{ where } \varepsilon_i^N \sim N\left(0, (\sigma_j^N)^2\right)$$

$$\delta^2 H_{ij}^{obs} = \delta^2 H_j + \varepsilon_i^H \text{ where } \varepsilon_i^H \sim N\left(0, (\sigma_j^H)^2\right)$$

The likelihood for this model for $i = 1$ to m individuals, and $j = 1$ to n species groups is:

$$\begin{aligned} L(x|\varphi, y, \sigma) = & \prod_{i=1}^m \prod_{j=1}^n \left(\frac{1}{\sigma_j^C \sqrt{2\pi}} \exp \left[\frac{1}{2(\sigma_j^C)^2} (\delta^{13} C_{ij}^{obs} - \delta^{13} C_j)^2 \right] \right) \times \\ & \prod_{i=1}^m \prod_{j=1}^n \left(\frac{1}{\sigma_j^N \sqrt{2\pi}} \exp \left[\frac{1}{2(\sigma_j^N)^2} (\delta^{15} N_{ij}^{obs} - \delta^{15} N_j)^2 \right] \right) \times \\ & \prod_{i=1}^m \prod_{j=1}^n \left(\frac{1}{\sigma_j^H \sqrt{2\pi}} \exp \left[\frac{1}{2(\sigma_j^H)^2} (\delta^2 H_{ij}^{obs} - \delta^2 H_j)^2 \right] \right) \end{aligned} \quad (11)$$

2.9.1.6 Prior Distributions

We used prior information and sample data to estimate posterior distributions of model parameters (Table S2.1). To calculate trophic position, we assumed a normal distribution of $\delta^{15}\text{N}$ in baseline consumers with a mean and SD equal to that of sampled calanoid copepods. Basal sources include $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of POM or phytoplankton. We assumed offshore sources were normally distributed with published mean and SD of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in bulk suspended POM measured in the upper 100 m at Ocean Station P in the GOA^{16,17}. These data are in line with data for primary consumers (copepods, $\delta^{13}\text{C} = -23.3$ SD 2.0‰; $\delta^{15}\text{N} = 7.3$ SD 2.5‰, $n = 1590$) in the GOA¹⁸. Coastal source $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were assumed to have a normal distribution with mean and SD of three bulk plankton samples (this study) in coastal marine waters that we assumed to be primarily composed of phytoplankton based on their green coloration, high chlorophyll *a* concentrations (Arimitsu, unpublished data) and $\delta^{15}\text{N}$ values consistent with trophic level = 1. Glacial freshwater source $\delta^{13}\text{C}$ was assumed to be normally distributed with the published mean and SD of riverine OM $\delta^{13}\text{C}$ throughout the world¹⁹. These values aligned with glacier-derived

riverine OM $\delta^{13}\text{C}$ values sampled in this study, although one glacial freshwater sample had higher riverine OM $\delta^{13}\text{C}$ compared to other sites and other glacier streams in Alaska (Table S2.2, Fellman unpublished data) it still fell within the expected SD of published world riverine OM $\delta^{13}\text{C}$ values. Riverine OM $\delta^{15}\text{N}$ was assumed to be normally distributed with the mean and SD of samples measured in this study.

Basal sources of $\delta^2\text{H}$ were the measured $\delta^2\text{H}$ abundance of water in offshore marine, coastal marine and glacial freshwater. We assumed offshore, coastal and freshwater $\delta^2\text{H}$ sources were normally distributed with a mean and SD of water sampled in the Aleutian Islands, Prince William Sound coastal waters (> 50 m depth and salinity > 28 to exclude surface waters with freshwater influence), and glacial streams above the tideline in Prince William Sound (Table S2.1-S2.2).

We assumed trophic discrimination factors of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ varied by taxa and tissue (i.e., bird liver, bird blood, whole fish, fish muscle, macro- and microzooplankton whole invertebrate) sampled²⁰. We assumed per-trophic level discrimination factors were normally distributed with mean of 0.4 ‰ (SD 1.3) for $\Delta^{13}\text{C}_k$ ^{21,22} and between 2.2 and 3.2 ‰ (SD range 0.07 – 1.9) for $\Delta^{15}\text{N}_k$ (Table S2.1) depending on tissue type based on data from similar taxa-tissue types²⁰. Lower and upper bounds of trophic position were set between 2 and 5. Due to the difficulty of isolating $\delta^2\text{H}$ abundance in the autotrophic component of riverine OM we used indirect methods to estimate photosynthetic fractionation between $\delta^2\text{H}$ in water and that of primary consumers following the work of others²³. Photosynthetic fractionation ($\Delta^2\text{H}$) between phytoplankton and water was assumed to be normally distributed with a mean of -163.7 ‰ (SD 27.9‰), which corresponds to values reported from freshwater and marine systems^{11,13,12,23,24}. Our lipid-free estimates of $\Delta^2\text{H}$ from 3 coastal phytoplankton (> 150 μ) samples had a mean of -

140.5 ‰ (SD 27.2, Table S2.2). Laboratory studies suggest the proportion of $\delta^2\text{H}$ in consumer tissues due to environmental water ranges from 0.33 – 0.41 for fish¹⁵ and from 0 – 0.39 across trophic levels in aquatic systems¹⁴. To account for trophic compounding of environmental water we applied the following priors for the ω parameters by species group: normal priors with a mean of 0.33 and standard deviation of 0.1 for fish, and normal priors with mean of 0.23 and standard deviation of 0.03²⁵ for zooplankton. Due to their higher trophic levels (τ), we applied the concept of trophic compounding¹⁴ to estimate ω for seabirds, such that $\omega_{seabird} = 1 - (1 - 0.23)^{\tau-1}$, but constrained the values of this parameter to a max of 0.60 as multiple lines of evidence suggest there is an upper limit to the proportion of tissue ^2H ^{14,25}.

We applied an uninformative uniform prior for f_{BLKI}^H between 30 and 150 ‰ based on exploratory data analysis. Standard deviations for source and fractionation were given a uniform prior from 0 to 10000.

Markov chain Monte Carlo (MCMC) was run for 10^6 iterations, with a burn-in of 10^5 iterations, and a thinning rate of 900 resulting in 1000 samples of the posterior distribution. We used Stan²⁶ implemented in R v. 3.1.2²⁷. We chose this software over others (e.g. JAGS, WinBUGS) because it compiles into C++ programming language, and also handles complex models more efficiently by implementing a gradient-based No-U-Turn sampling system²⁸. Visual inspection of trace plots for model parameters indicated adequate convergence of model parameters, and posterior predictive distributions were evaluated to assess model fit (Fig. S2.1-S2.4).

2.9.1.7 Implications of an integrated food web Bayesian isotope mixing model

We developed a Bayesian isotope mixing model informed both by prior information on source and discrimination of stable isotopes, as well as data from 14 coastal species. Our

Bayesian model accounts for uncertainty in source and discrimination parameters by treating them as random variables with probability distributions, which is of paramount importance in any isotope mixing model, but also contributes to wider 95% credible intervals compared to frequentist methods²⁹. This model was similar to models developed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes that can be reasonably attributed completely to diet and in which we assume conservative mixing with step-wise trophic enrichment^{30,31}. To date, there is no existing mixing model software designed to handle the added complexities of ^2H isotopes and so our model includes a key modification^{14,23} to account for the proportion of ^2H in consumer tissues due to environmental water. We accounted for the proportion of tissue ^2H due to water and apparent trophic enrichment^{14,15} using published information on $\delta^2\text{H}$ in aquatic systems and incorporated uncertainty in this parameter for each species using Bayesian inference. The posterior distribution of the photosynthetic fractionation of $\delta^2\text{H}$ parameter had a mean of -139.2 ‰ (95% credible interval: -154.9 to -121.6 ‰), which was well aligned with our lipid-free marine phytoplankton samples (Table S2.2). Model estimates suggest that abundance of ^2H in black-legged kittiwake liver tissue was enriched by 59.2 ‰ (44.5 – 73.8 ‰) compared to other species (tissues) we sampled. This may be due to tissue-specific isotopic discrimination which is currently poorly known for ^2H in food webs but which is seen in other isotopes³². Alternatively this additional source of ^2H discrimination in black-legged kittiwakes, also noted in other seabird species³³, may be due to a metabolic process unique to seabirds whereby excess salt excretion occurs through the salt glands³⁴, although further study is required to understand the mechanism and magnitude of this effect.

2.9.1.8 References

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Table S2.1. Parameters and priors for 3-source Bayesian isotope mixing model. Normal distributions are denoted as N(mean, SD), and uniform priors are denoted as U(min, max).

Parameter		Isotope	Prior	Comments
Baseline Consumer	Copepod	$\delta^{15}\text{N}$	N(7.03, 1.38)	copepod, measured this study, n = 4
Source	Offshore Marine	$\delta^{13}\text{C}$	N(-24.2, 0.8)	< 100 m POM, Ocean Station P ¹⁶ , n = 4
		$\delta^{15}\text{N}$	N(3.6, 0.2)	POM, Ocean Station P ¹⁷ , n = 3
		$\delta^2\text{H}$	N(-7.4, 1.0)	water measured this study, n = 3
	Coastal Marine	$\delta^{13}\text{C}$	N(-19.1, 1.2)	POM measured this study, n = 3
		$\delta^{15}\text{N}$	N(3.1, 0.6)	POM measured this study, n = 3
		$\delta^2\text{H}$	N(-15.3, 3.6)	water measured this study, n = 10
	Glacial Freshwater	$\delta^{13}\text{C}$	N(-26.4, 1.5)	Riverine POM ¹⁹
		$\delta^{15}\text{N}$	N(4.4, 3.9)	POM, measured this study, n = 3
		$\delta^2\text{H}$	N(-113.0, 10.9)	water, measured this study, n = 4
Discrimination	$\Delta\text{C}_{\text{all tissues}}$	$\delta^{13}\text{C}$	N(0.4, 1.3)	²¹
	$\Delta\text{N}_{\text{bird-liver}}$	$\delta^{15}\text{N}$	N(3.0, 0.9)	²⁰ n = 3
	$\Delta\text{N}_{\text{bird-blood}}$	$\delta^{15}\text{N}$	N(2.2, 0.7)	²⁰ n = 5
	$\Delta\text{N}_{\text{fish-muscle}}$	$\delta^{15}\text{N}$	N(3.2, 1.9)	²⁰ n = 10
	$\Delta\text{N}_{\text{whole-fish}}$	$\delta^{15}\text{N}$	N(2.2, 1.1)	²⁰ n = 3
	$\Delta\text{N}_{\text{whole-inverts}}$	$\delta^{15}\text{N}$	N(2.3, 0.9)	²⁰ n = 5
	$\Delta^2\text{H}$	$\delta^2\text{H}$	N(-163.7, 27.0)	^{13,12,23}
	$f_{\text{blki}}^{\text{H}}$	$\delta^2\text{H}$	U(30, 150)	
Proportion of consumer tissues due to water	ω_{bird}	$\delta^2\text{H}$	N(1-0.77 ^($\tau-1$) , 0.02)	^{14,25,29,30}
	ω_{fish}	$\delta^2\text{H}$	N(0.33, 0.1)	^{25,30}
	$\omega_{\text{zooplankton}}$	$\delta^2\text{H}$	N(0.23, 0.03)	^{14,25}
SD	sources, discrimination	$\delta^{13}\text{C}$	U (0, 10000)	
		$\delta^{15}\text{N}$	U (0, 10000)	
		$\delta^2\text{H}$	U (0, 10000)	

Table S2.2. Stable isotope composition (‰), C:N ratio (runoff only), photosynthetic fractionation (Δ^2H , coastal marine only) and nutrient concentration (μM) in glacier runoff and coastal marine source samples. Abbreviations: particulate organic matter, POM; phytoplankton, Phyto; dissolved inorganic matter, DIC; phosphate, PO_4 ; silicic acid, $SiOH_4$; nitrate, NO_3 ; nitrite, NO_2 , ammonium, NH_4 .

Riverine OM	POM- $\delta^{13}C$	POM- $\delta^{15}N$	POM-C:N	DIC- $\delta^{13}C$	δ^2H_{Water}	$\delta^{18}O_{Water}$	PO_4	$SiOH_4$	NO_3	NO_2	NH_4
Blackstone	-26.3	2.1	8.3	-8.6	-112.1	-16.0	0.18	0.82	0.12	0.02	0.86
Columbia	-26.0	2.3	6.8	-5.0	-128.6	-17.0	2.80	11.32	0.56	0.58	2.35
Icy Bay	-22.5	8.9	5.5	-9.9	-104.4	-14.3	0.92	6.06	0.20	0.14	3.98
Coastal Phytoplankton	Phyto- $\delta^{13}C$	Phyto- $\delta^{15}N$	Phyto- δ^2H	Δ^2H^*	δ^2H_{Water}	$\delta^{18}O_{Water}$	PO_4	$SiOH_4$	NO_3	NO_2	NH_4
Blackstone	-19.9	2.5	-175.1	-123.8	-37.3	-5.4	0.52	2.46	0.13	0.14	1.86
Columbia	-19.6	3.1	-214.5	-171.9	-36.1	-4.4	1.26	8.22	3.64	0.18	0.62
Icy Bay	-17.7	3.6	-162.1	-125.8	-32.3	-4.2	1.71	15.73	9.59	0.26	0.41

*

$$\Delta^2H = (\delta^2H_{POM} - \delta^2H_{water}) \div \left(1 - \frac{\delta^2H_{water}}{1000}\right)$$

Table S2.3. Mean (SD) of posterior distributions for trophic position and source contributions to each species.

Taxon	Species	Trophic Position	Offshore Marine	Coastal Marine	Riverine OM
Seabird	Black-legged kittiwake	4.5 (0.2)	0.34 (0.20)	0.36 (0.20)	0.30 (0.16)
Seabird	Kittlitz's murrelet	4.2 (0.1)	0.29 (0.13)	0.28 (0.14)	0.43 (0.10)
Seabird	marbled murrelet	4.3 (0.1)	0.49 (0.14)	0.34 (0.15)	0.17 (0.08)
Fish	capelin	3.7 (0.1)	0.46 (0.14)	0.32 (0.11)	0.22 (0.11)
Fish	eulachon	4.2 (0.1)	0.31 (0.15)	0.34 (0.13)	0.35 (0.15)
Fish	Pacific herring	3.8 (0.1)	0.49 (0.17)	0.26 (0.11)	0.25 (0.15)
Fish	walleye pollock	3.8 (0.1)	0.26 (0.15)	0.42 (0.12)	0.32 (0.15)
Fish	Pacific sand lance	3.5 (0.1)	0.39 (0.16)	0.29 (0.11)	0.32 (0.15)
YOY fish	YOY capelin	3.3 (0.1)	0.39 (0.15)	0.31 (0.12)	0.30 (0.14)
YOY fish	YOY Pacific herring	3.3 (0.1)	0.36 (0.17)	0.20 (0.12)	0.44 (0.16)
YOY fish	YOY walleye pollock	3.3 (0.1)	0.19 (0.13)	0.43 (0.13)	0.39 (0.14)
Macrozooplankton	<i>Euphausia pacifica</i>	3.1 (0.1)	0.54 (0.11)	0.28 (0.10)	0.18 (0.09)
Macrozooplankton	<i>Neomysis rayii</i>	3.5 (0.1)	0.66 (0.12)	0.21 (0.12)	0.12 (0.07)
Macrozooplankton	<i>Themisto libellula</i>	3.2 (0.1)	0.37 (0.11)	0.50 (0.10)	0.14 (0.07)
Macrozooplankton	<i>Thysanoessa</i> sp.	2.8 (0.1)	0.12 (0.08)	0.51 (0.10)	0.36 (0.09)
Microzooplankton	Bulk Zooplankton	2.1 (0.1)	0.15 (0.11)	0.40 (0.14)	0.45 (0.12)
Microzooplankton	Copepod	2.0 (1.1)	0.38 (0.15)	0.43 (0.15)	0.19 (0.10)

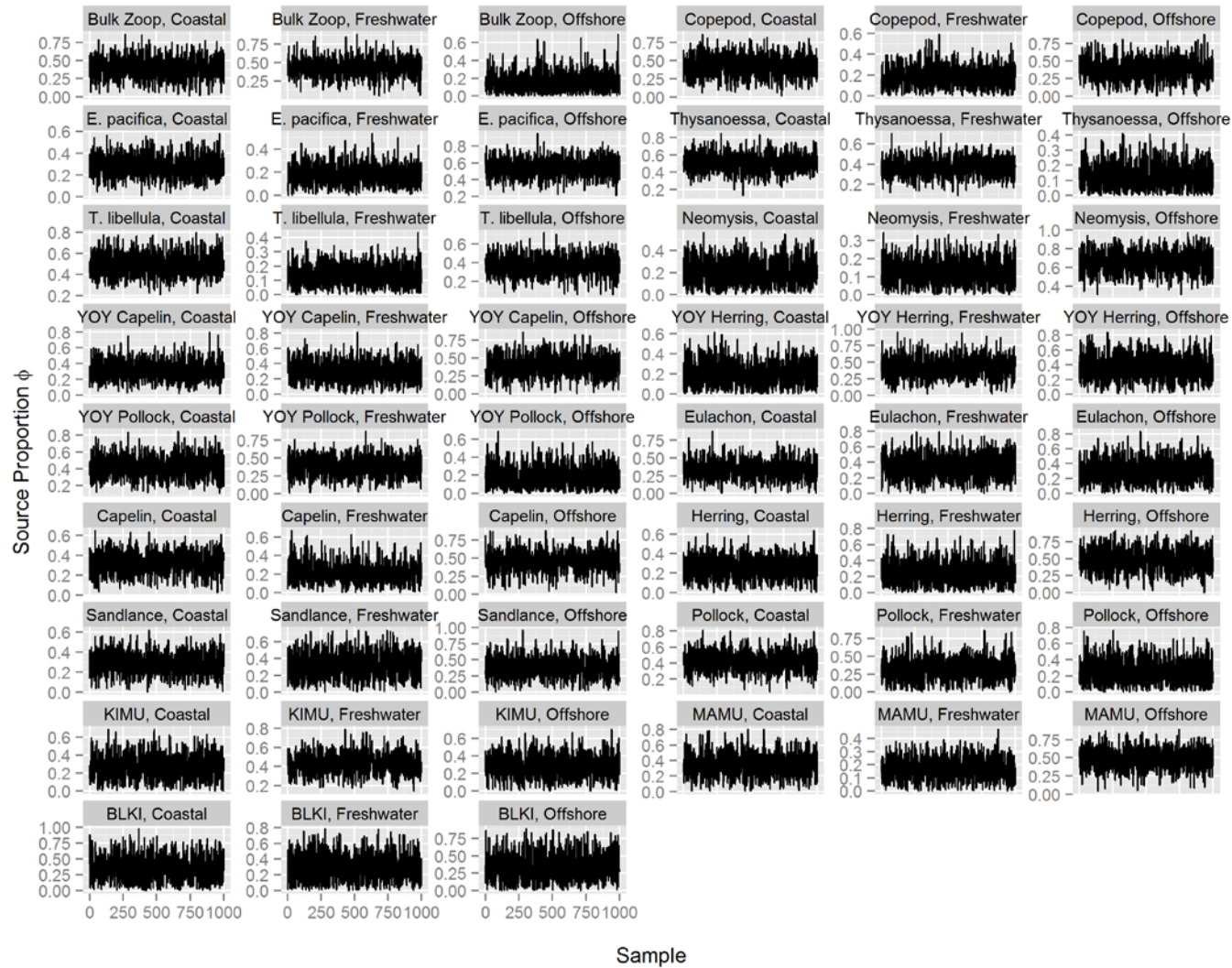


Fig. S2.1. MCMC trace plots of source contribution parameters for each species group sampled in the glacial-marine habitat. Abbreviations: young of the year (YOY), Kittlitz's murrelet (KIMU), marbled murrelet (MAMU), black-legged kittiwake (BLKI).

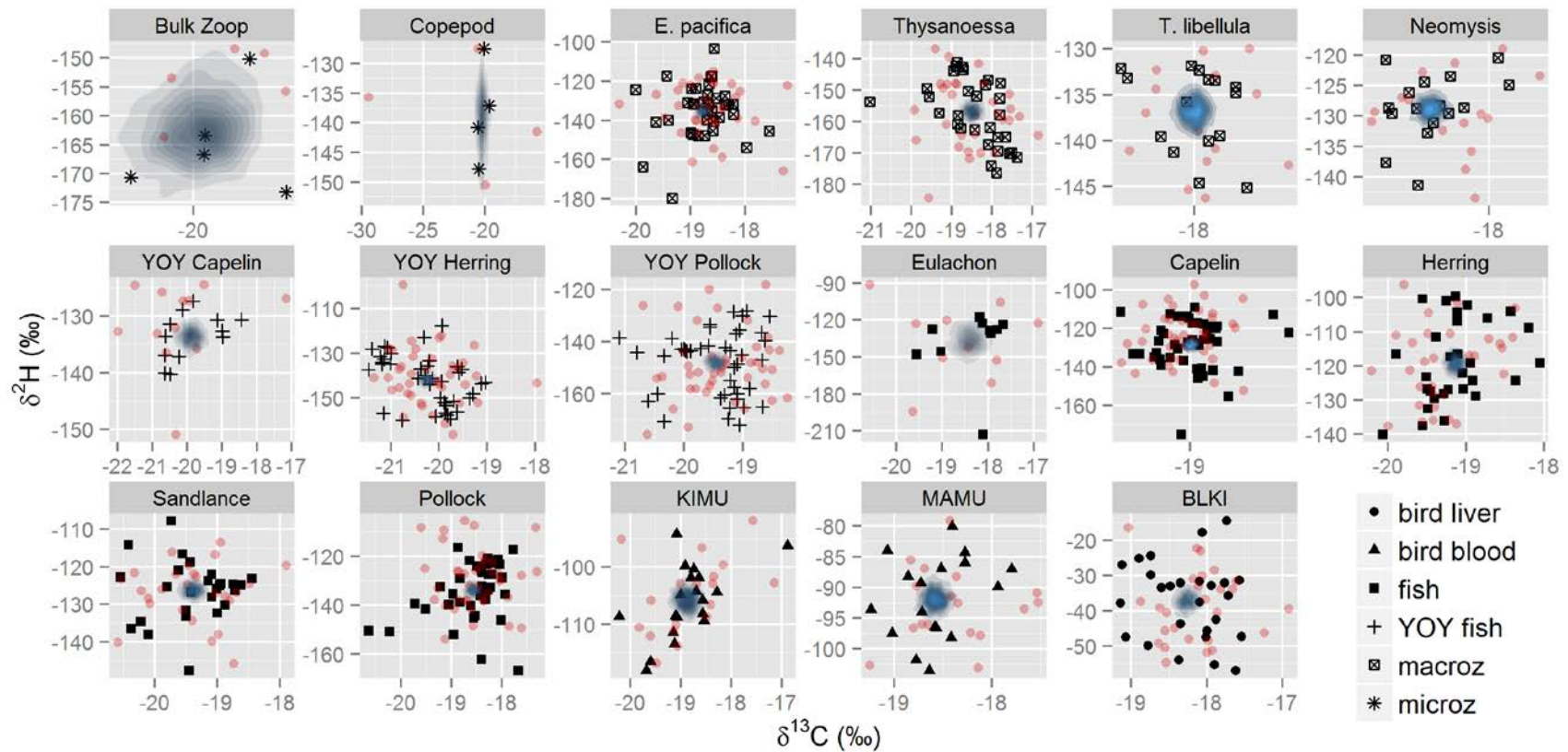


Fig. S2.2. Observed (black symbols) vs expected (kernel density contours of posterior distributions) $\delta^{13}\text{C}$ and $\delta^2\text{H}$ values for each species group. Greater opacity indicates higher density contours. Posterior predictive distributions for $\delta^{13}\text{C}$ and $\delta^2\text{H}$ are shown as light red circles. Abbreviations: young of the year (YOY), Kittlitz's murrelet (KIMU), marbled murrelet (MAMU), black-legged kittiwake (BLKI).

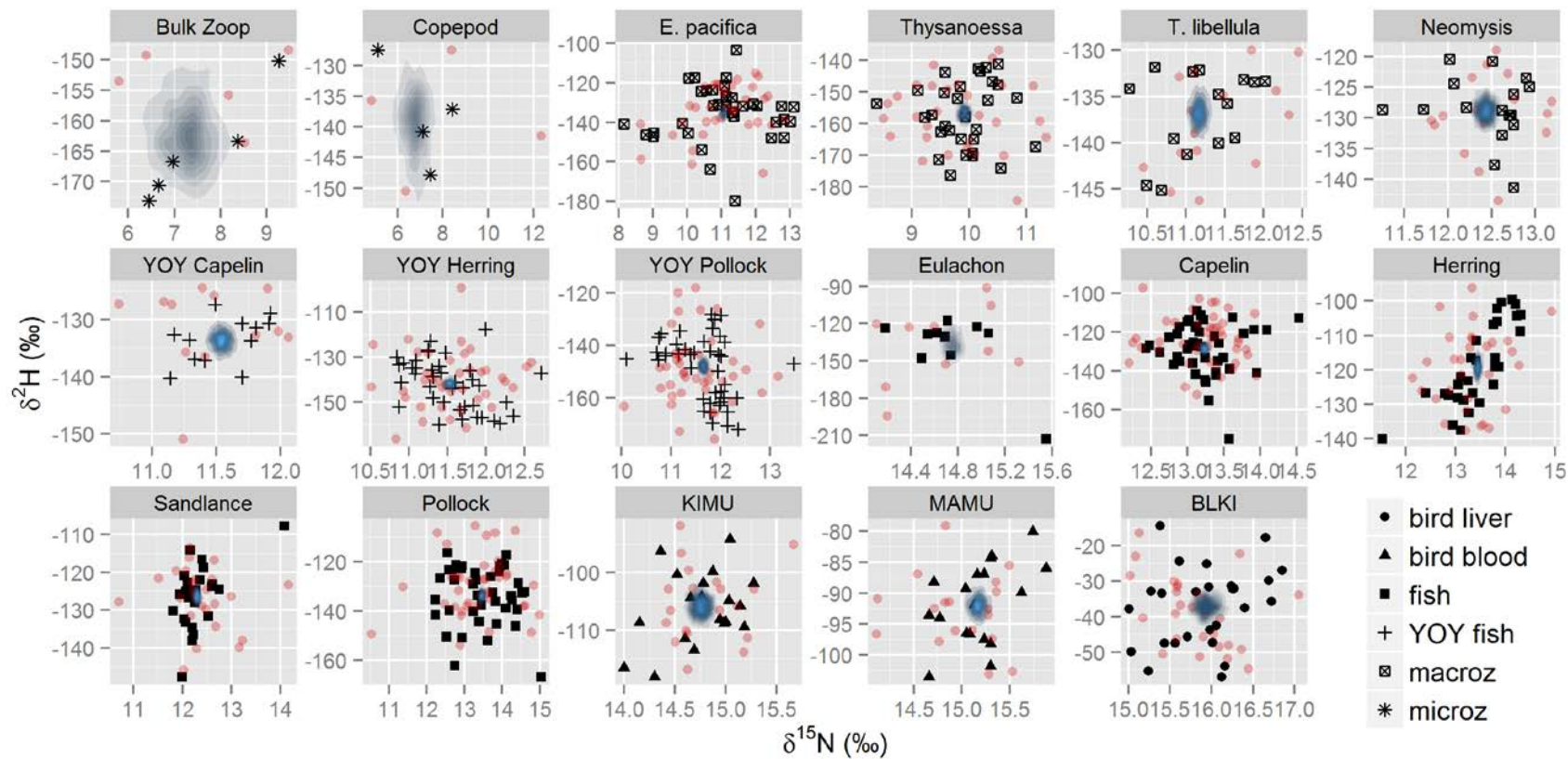


Fig. S2.3. Observed (black symbols) vs expected (kernel density contours of posterior distributions) $\delta^{15}\text{N}$ and $\delta^2\text{H}$ values for each species group. Greater opacity indicates higher density contours. Posterior predictive distributions for $\delta^{15}\text{N}$ and $\delta^2\text{H}$ are shown as light red circles. Abbreviations: young of the year (YOY), Kittlitz's murrelet (KIMU), marbled murrelet (MAMU), black-legged kittiwake (BLKI).

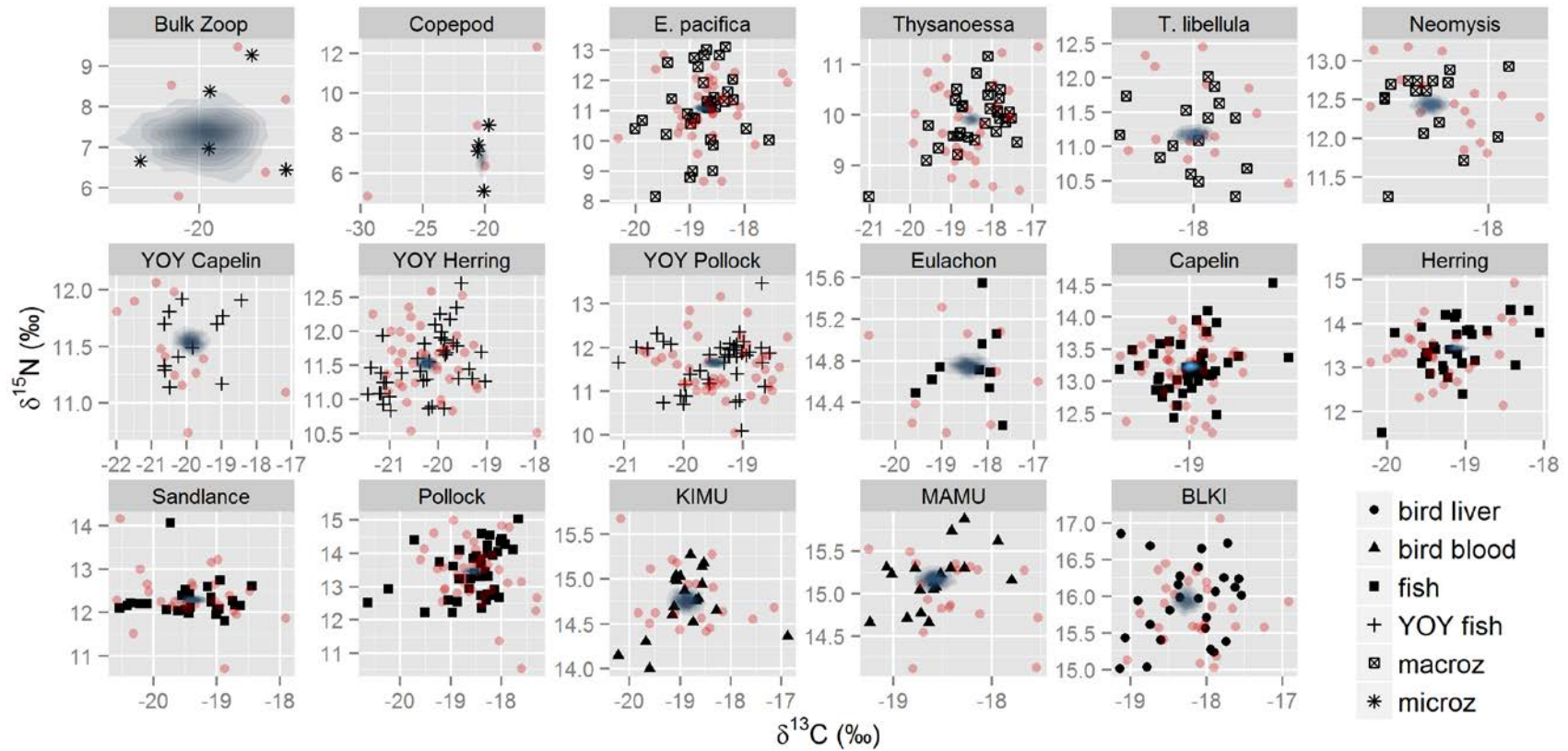
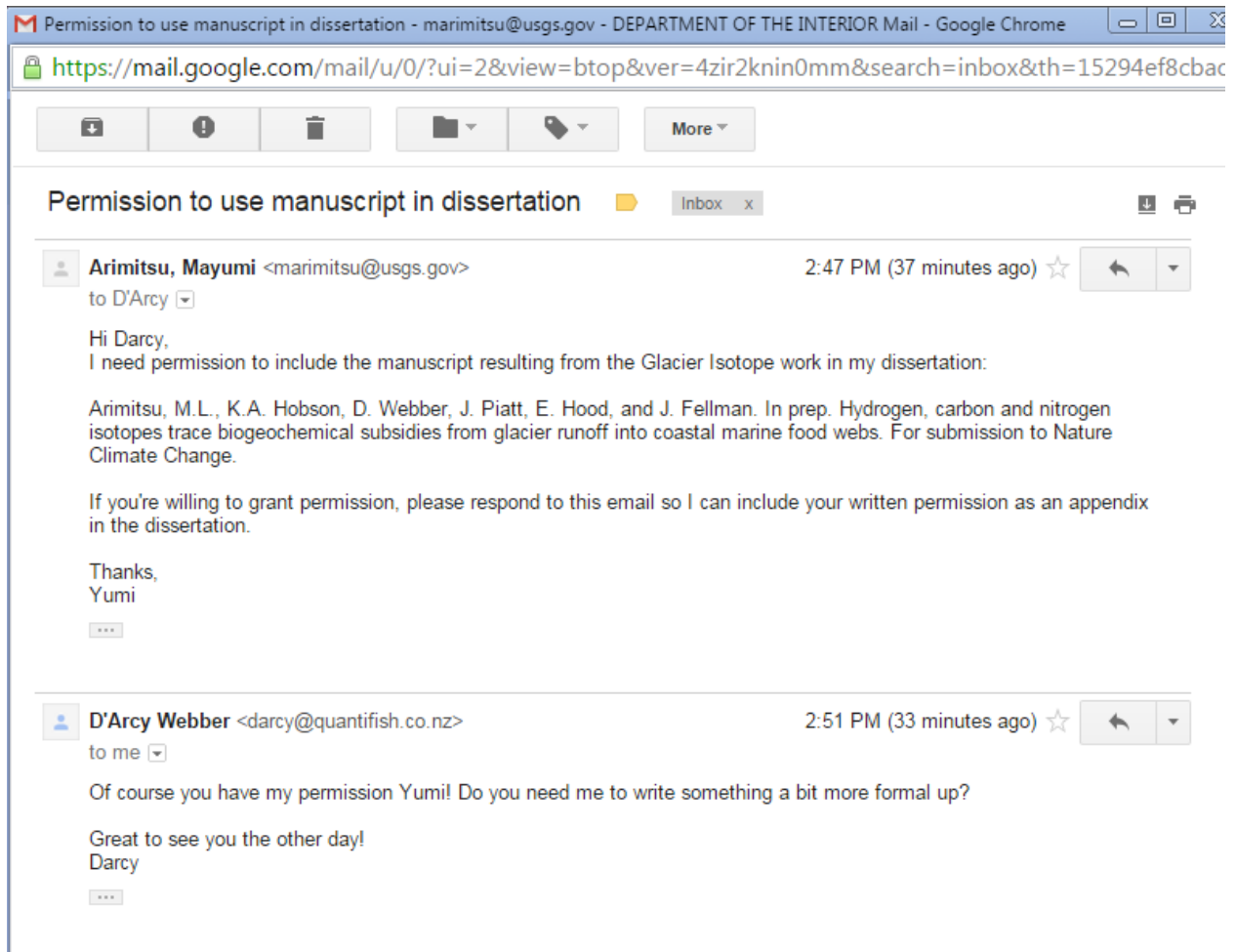
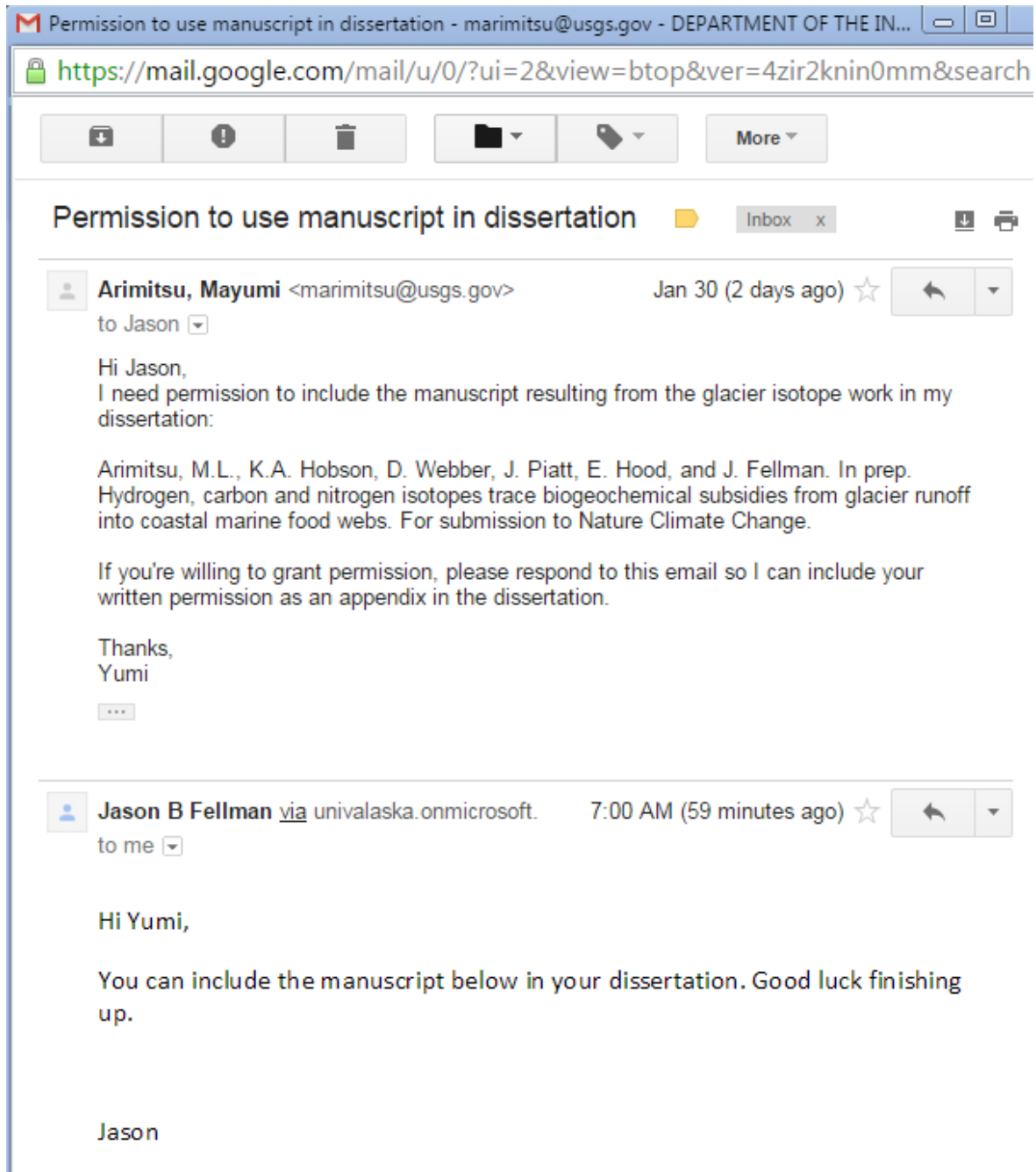


Fig. S2.4. Observed (black symbols) vs. expected (kernel density contours of posterior distributions) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each species group. Greater opacity indicates higher density contours. Posterior predictive distribution $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are shown as light red circles. Abbreviations: young of the year (YOY), Kittlitz's murrelet (KIMU), marbled murrelet (MAMU), black-legged kittiwake (BLKI).

Appendix 2.9.2 Permission to use manuscript in dissertation from D'Arcy Webber



Appendix 2.9.3 Permission to use manuscript in dissertation from Jason Fellman



Appendix 2.9.4 IACUC approval letter



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Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

July 24, 2013

To: Franz Mueter
Principal Investigator
From: University of Alaska Fairbanks IACUC
Re: [469319-3] Tracing the flow of terrestrial organic nutrients and ancient glacial carbon through coastal marine food webs

The IACUC reviewed and approved the Amendment/Modification referenced above by Full Committee Review.

Received:	July 24, 2013
Approval Date:	July 24, 2013
Initial Approval Date:	July 24, 2013
Expiration Date:	July 24, 2014

This action is included on the August 15, 2013 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Chapter 3. Scale-dependent influence of glaciers on marine ecosystems in the Gulf of Alaska

3.1 Introduction

3.2 Glacial influence on the marine ecosystem

Melting glaciers are well documented and unequivocal indicators of global warming on Earth (IPCC 2014). Alaska's glaciers comprise about 13 % of the world's mountain glaciers and they are among the largest continuous ice masses in high-latitude temperate ecosystems (Arendt et al. 2002). About 16% of the Gulf of Alaska watershed is covered in glacier ice (O'Neel et al. 2015). Currently in the Gulf of Alaska region 37 glaciers terminate at or close to sea level (so-called tidewater glaciers, McNabb & Hock 2014), often in deep fjords created by glacial retreat. Alaska has 200 major fjords, and these fjords provide important wintering, breeding, nursery and feeding areas for marine organisms, including top-level marine birds and mammals and commercially important fish and shellfish (Piatt & Gende 2007; Nielsen et al. 2007; Arimitsu et al. 2012).

Drivers of glacier volume change include the magnitude of summer air temperatures (solar radiation and sensible heat available for melting), and winter snowfall (accumulation). For tidewater glaciers, the instability of the glacier face additionally causes increased calving rates and rapid rates of mass loss (O'Neel 2005, Larsen et al. 2007). The majority of glaciers in Alaska are thinning and retreating; however, tidewater glaciers, which comprise roughly 14% of the total area of glacier ice in the region, are subject to greater variability because of their low elevation relative to equilibrium-line altitudes (Larsen et al. 2007, McNabb & Hock 2014). In contrast to tidewater glacier dynamics, which can be dominated by calving processes, mass balance of land-terminating alpine glaciers are more directly coupled to climate (Post et al. 2011, Larsen et al. 2015).

Rates of mass loss for Alaska's glaciers over recent decades have been estimated to range from 46 - 75 Gt yr⁻¹ (Jacob et al. 2012, Arendt et al. 2013, Hill et al. 2015, Larsen et al. 2015) and are among the highest on earth. Rapid wastage of glaciers in coastal Alaska is contributing to rising global sea level and high rates of sedimentation from silty glacial river outflows (Arendt et al. 2002, Larsen et al. 2005). Roughly 47 % of the annual freshwater runoff into the Gulf of Alaska drains from glacial landscapes (Neal et al. 2010). Along with abundant rainfall and wind, glacial runoff creates a steep cross-shelf density gradient that drives the Alaska Coastal Current (ACC) and influences zooplankton abundance and salmon production in nearshore regions (Royer et al. 2001).

The Gulf of Alaska is a highly productive large marine ecosystem (LME, Sherman 1991) with abundant fish and wildlife resources (Hood & Zimmerman 1987) that fuel economically important fisheries and tourism industries (McDowell Group 2015, Fissel et al. 2015). Much of the general physical and biogeochemical influence from icefields to ocean has been described recently for the North Pacific coastal temperate rainforest (reviewed in O'Neel et al. 2015). However, we lack a basic understanding of how predicted changes in the timing and magnitude of glacial freshwater flux into the marine ecosystem will effect primary productivity, predator-prey interactions, and humans in coastal areas.

Here I examined the influence of glaciers on the marine environment and the trophic ecology of coastal marine food webs at varying spatial scales in the Gulf of Alaska. Similar to most ecological patterns in nature (Levin 1992), the influence of glaciers on coastal habitat, biological communities and humans depends on the spatial and temporal scale of interest. The purpose of this work was to synthesize information on the influence of glaciers on marine habitat, lower-trophic level productivity, predator-prey interactions and humans in the Gulf of

Alaska marine ecosystem at local (< 10 km), meso- (< 100 km) and basin (1000s km) spatial scales. I synthesized information on food-web dynamics within tidewater glacier plumes. I also used hydroacoustic data to illustrate the vertical and horizontal distribution of prey near glacial features (e.g., tidewater glaciers, terminal moraines) in fjords of Alaska. I then summarized the importance of glacier melt water in large-scale circulation and the role of essential micronutrient enrichment to offshore waters in the Gulf of Alaska. Finally, I provided evidence from the paleoenvironment that describes productivity peaks associated with melt water influence, sea level change, and iron enrichment in the North Pacific during glacial-interglacial periods in the Pleistocene and Holocene eras. At each scale I summarized the influence of glaciers on habitat gradients, marine food webs and, where relevant, discussed how humans may be affected by anticipated ecological change.

3.2.1 Glacier runoff plume dynamics

Local scale effects of glacier runoff on the marine ecosystem, including habitat, species composition, behavior and trophodynamics of marine communities, are observed within the turbid glacier plume within 10 km of tidewater glaciers or glacier river sources. The surface lens within the plume waters are characterized by low temperature, low salinity, high stratification, generally elevated nutrient concentrations and high turbidity due to fine glacier sediment in runoff (Fig. 3.1, Arimitsu et al. 2012, chapter 1).

Sediment-laden melt water restricts light penetration into the water column, which has negative effects on phytoplankton abundance (Piwosz et al. 2008, Arimitsu et al. 2012, Meire et al. 2015). Relatively high phaeopigment to chlorophyll a ratios in the glacier plume waters of Glacier Bay suggest that phytoplankton biomass was composed of older horizontally advected

cells, rather than larger ($> 10 \mu\text{m}$ size fraction) younger cells in an active growth phase that dominated warmer waters of the bay with greater light penetration (Lisa Eisner, pers. comm.).

The low ratio of autotrophic (e.g., phytoplankton) to heterotrophic (e.g. microbial) productivity observed in glacial melt water plumes led Chilean researchers to question whether food webs in these systems rely heavily on terrestrial-derived energy sources (Vargas et al. 2008, 2011, Silva et al. 2011). They hypothesized that high quality autotrophic biomass in glacier plumes is not sufficient to support the classical (i.e., phytoplankton-based) marine food web (Vargas et al. 2011). They found that 50-90% of the allochthonous organic matter in fjords is associated with local river discharge (Silva et al. 2011), and the contribution of terrestrial-derived organic carbon to marine copepods in Chilean glacial fjords is between 20 – 61 % (Vargas et al. 2011, Lafon et al. 2014).

Similarly, the contribution of riverine organic matter to the pelagic marine food web near the glacier-marine interface in Gulf of Alaska fjords was moderate, ranging from 12 to 45 % in 14 species groups (Fig. 3.2). On the high end of these estimates were bulk zooplankton (45%), *Thysanoessa* spp. (krill, 36%), eulachon (*Thaleichthys pacificus*, fish, 35%), young of the year walleye pollock (*Gadus chalcogrammus*, fish, 39%), young of the year herring (*Clupea pallasii*; fish, 44%) and Kittlitz's murrelet (*Brachyramphus brevirostris*, seabird, 43%). In contrast, species on the low end of these estimates include *Neomysis rayii*, *Themisto libellula* and *Euphausia pacifica* (crustaceans: mysid, amphipod and krill; 12%, 14% and 18%, respectively), and the marbled murrelet (*B. marmoratus*, seabird, 17%). Higher use of riverine organic matter by species that spend the most time foraging in the glacier plume suggests relatively strong terrestrial-marine linkages in this pelagic marine food web. The contrast in riverine organic

matter use among species was likely related to the amount of time spent foraging within the glacier plume where in situ productivity is low (see Chapter 2).

Although low chlorophyll a conditions prevail in the melt water plume, there is typically a scattering layer of krill, forage fish (capelin *Mallotus villosus*, eulachon, Pacific herring, Northern lampfish *Stenobrachius leucopsaurus*) and juvenile or adult walleye pollock in the upper 30 to 50 m of the water column (Renner et al. 2012, Arimitsu et al. 2012, chapter 1), where cold dark conditions mimic those found in deeper water even during daylight hours.

Hydroacoustic and trawl data indicate that a persistent shallow layer of krill and fish occurs above the pycnocline (see representative example in Fig. 3.3) where water clarity is low and fish are diffuse in the glacier plume (Womble et al. 2014).

High turbidity in the glacier plume affects the depth and density distribution of krill and planktivorous fish that typically undergo diurnal vertical migration (DVM) behavior. During normal DVM zooplankton and their predators migrate from deep to shallow water column depths in response to lower light intensity at night time (Cushing & Harden Jones 1968, Hays 2003). In the glacial plume waters, however, mesopelagic species (e.g. krill, northern lampfish) that are known to regularly undergo DVM occur in the surface waters during daylight hours (Abookire et al. 2002, Renner et al. 2012, Arimitsu et al. 2012). Planktivorous feeding fish like capelin and walleye pollock also feed primarily on krill and other crustaceans in the plume waters (Robards et al. 2003). De Robertis et al. (2003) found that planktivorous fish were less sensitive than piscivorous fish to vision impairment issues in waters of increasing turbidity, and that turbid environments may be favorable for planktivores because they are less vulnerable to attack by predators.

Some marine predators routinely exploit glacier plumes for feeding and breeding activities. Surface-feeding seabirds such as black-legged kittiwakes (*Rissa tridactyla*) and Arctic terns (*Sterna paradisaea*) exploit prey resources brought to the surface by calving ice or upwelled subglacial discharge (Lydersen et al. 2014) or osmotic shock (Weslawski & Legezynska 1998). Kittiwakes build their nests in colonies on cliffs next to tidewater glaciers (Hooge 1995, Suryan & Irons 2001), and Arctic terns and Aleutian terns (*Onychoprion aleuticus*) nest in glacial outwash areas that provide suitable ground-nesting habitat (Arimitsu et al. 2007a). Although these species are widely distributed and use productive non-glacial habitats of Alaska, they appear to benefit from prey resources in plume waters and breeding habitat near glaciers as well.

In contrast to species that are widely distributed across a variety of marine habitats, a large fraction (66%) of the global population of Kittlitz's murrelets occur in glaciated fjords and embayments of the coastal Gulf of Alaska during spring and summer (U.S. Fish and Wildlife Service 2013). These small diving seabirds forage on krill and small fish within the turbid glacier plume or in association with marine sills (Day et al. 2000, Arimitsu et al. 2012, Allyn et al. 2012). Perhaps the most important reason Kittlitz's murrelets migrate to fjords in the Gulf of Alaska each spring is because they nest in recently exposed post-glacial landscapes (Kissling et al. 2015). They nest solitarily on the ground, on cliff ledges or scree slopes in glaciated or recently deglaciated landscapes up to 45 km inland (U.S. Fish and Wildlife Service 2013). As a species, the Kittlitz's murrelet probably emerged during the early Pleistocene (Friesen et al. 1996) and evolved over a time of changing glacier coverage. Their life history includes glacial or recently deglaciated landscapes, which may explain their strong affinity to foraging conditions

within turbid plume waters throughout southern coastal Alaska (Allyn 2012, Arimitsu et al. 2012)

Harbor seals in fjords of Alaska use floating ice as haul out substrate during the pupping season, but they forage long distances from their ice haul outs, dive deeper and feed on more pelagic prey compared to harbor seals on terrestrial haul outs (Herreman et al. 2009, Blundell et al. 2011, Womble et al. 2014). Although their preferred prey species occur near ice haul out habitat (Arimitsu et al. 2007b, Herreman et al. 2009, Renner et al. 2012), the low-density foraging conditions within glacier plumes apparently provide sub-optimal foraging habitat for this predator species (Womble et al. 2014). An important trade-off, however, is that the ice haul out substrate provides protection from killer whale predators during pupping season (Blundell et al. 2011, Womble et al. 2014).

It has been suggested that harbor seal ice haul out sites near glaciers may also provide a predator refuge from transient killer whales. Pettit et al. (2015) found that ambient noise near tidewater glaciers ranged from 113 to 127 dB re: 1 μ Pa sound pressure levels and can be higher than any other natural oceanic noise. Although noise levels could provide acoustic protection for harbor seals, the glacier ambient noise spectral signature peaks between 1 and 3 kHz and falls below 80 dB at frequencies within the range of killer whale peak sensitivity (i.e., 18-42 kHz, Szymanski et al. 1999). Furthermore, these intelligent predators have demonstrated they are capable of adapting their foraging strategy to employ visual cues for prey capture in noisy ice environments, for example, wave washing cooperative hunting behavior by Antarctic pack ice killer whales (Pitman & Durban 2012). The AT1 population of transient killer whales regularly occurs well inside glaciated fjords in the Northern Gulf of Alaska (Matkin et al. 2012) suggesting that noise levels there are not sufficient to deter killer whales.

At local scales glaciers are also integral to Alaska's \$3.9 billion tourism industry, which provides a connection between humans and the environment through experiences that have great potential to influence human perception of climate change. In 2013-14, Alaska saw more than 1.9 million visitors (McDowell Group, 2015). Nearly 1 in 4 state-wide visitors (roughly 480,000 and 550,000 people in summers of 2014 and 2015, respectively, John Neary, U.S. Forest Service, pers. comm.) took excursions to the Mendenhall Glacier, one of the most accessible glaciers in Juneau, Alaska. Likewise, in 2014 more than 770,000 people visited National Parks featuring tidewater glaciers in coastal Alaska (Kenai Fjords and Glacier Bay National Parks visitor use combined, <https://irma.nps.gov/Stats/>, accessed 12/31/2015). Thus glacier tourism in Alaska provides a uniquely accessible first-hand experience of the Earth's melting glaciers and ultimately promotes greater awareness of climate change.

In summary, local scale effects of glaciers on coastal marine food webs are limited to plume waters within about 10 km of glacier runoff sources (Fig. 3.4). Riverine organic matter subsidies can be substantial within the plume food web where in situ marine production may not be sufficient to fuel the coastal food web (Vargas et al. 2011, chapter 2). Prey communities are structured by the low-light condition that may suppress diel vertical migration in krill and mesopelagic forage fish. Predator species may utilize sub-optimal foraging conditions because of proximity to nesting habitat (black-legged kittiwakes, Kittlitz's murrelets) or to minimize predation risk (e.g., harbor seals). Glaciers are a significant tourism draw and thus are important to local and state economies. Furthermore, glacier tourism promotes human awareness of climate change.

3.2.2 Glacially modified fjord ecosystems

Meso- scale effects of glaciers on coastal marine food webs are defined by the strong environmental gradients induced by glacier runoff in fjords, generally within 100 km of tidewater glaciers or glacial river sources. Coastal fjords and bays are common along the Gulf of Alaska coast and are carved by past glacial ice movements. Many fjords are long and narrow, with constrictions that cause large tidal fluctuations (Hill et al. 2009, Arimitsu et al. 2012). Oceanographic versus estuarine conditions in fjords are regulated by whether they 1) are protected or exposed to oceanic waters (e.g., Harriman Fjord vs. Yakutat Bay), and 2) have a shallow sill that marks the position of previous glacier termini (e.g., Muir Inlet, Icy Bay, Columbia Bay). Complex topography and bathymetry resulting from glacial processes and large volumes of freshwater discharge define coastal habitat features important to marine communities at higher trophic levels (Hop et al. 2002, Renner et al. 2012, Arimitsu et al. 2012, chapter 1).

Freshwater input from both glacial and non-glacial sources is a driver of water column stability and circulation, and carries sediment and nutrients into the marine environment. Maximum rates of glacier meltwater discharge occur from June to September (Hill et al. 2015). Unlike offshore areas of the Gulf of Alaska, which are characterized by distinct spring (initiated by light availability, Strom et al. 2015) and fall blooms (initiated by nutrient renewal, Childers et al. 2005), phytoplankton abundance and net community production in some glacial fjords are high and sustained through the melt water season (Etherington et al. 2007, Meire et al. 2015, Reisdorph & Mathis 2015). During peak melt season in summer, steep horizontal gradients in nutrient concentration, water clarity, temperature, salinity and stratification (Fig. 3.1) describe much of the variability in chlorophyll *a* (an index of phytoplankton biomass) at the base of marine food webs (chapter 1).

Zooplankton biomass patterns in the fjords differed among protected versus exposed fjord systems in the Gulf of Alaska (see chapter 1) and appear to be heavily influenced by advective processes. Relatively higher biomass was found near glaciers in the more estuarine sites, but the opposite was true in fjords with more oceanic influence. In Kenai Fjords there are differences in abundance of oceanic vs. neritic copepod species between exposed and protected fjords (Arimitsu et al. 2012). Copepod abundance, distribution and community composition in fjords is probably driven by advection and water mass structure (Cooney et al. 2001, Hop et al. 2002, Walkusz et al. 2003), which is in turn strongly influenced by coastal geometry carved by the region's glacial history (Stabeno et al. 2015). The presence of a sill isolates cold fresh melt water in the basins behind them, where zooplankton may become entrapped and undergo mortality from osmotic shock in very low salinity waters (Weslawski & Legezynska 1998, Weslawski et al. 2000). Robards et al. (2003) found that zooplankton (composed mainly of Calanoid copepods) abundance increases and diversity decreases with distance up the fjords in Glacier Bay. They also showed that local processes influence copepod dynamics near the head of fjords, which differs from areas near the mouth of the bay where community dynamics are more related to oceanographic processes outside the mouth of the fjord.

In contrast to zooplankton, forage fish are more independent of currents because they can maintain their distribution in their preferred habitat. For example, capelin are an important cold-water forage fish, notable for their rapid and widespread response to thermal regimes (Anderson & Piatt 1999, Rose 2005, Hatch 2013). Their inshore migration and spawning aggregations provide a lipid-rich food source for avian, fish and marine mammal predators (Brown 2002, Sigler et al. 2009). In summer capelin spawn on beaches in the fjords where glacial melt water provides cold water refuge. Based on larval length frequencies and temporal variation in

maturation of ripe females, capelin in Glacier Bay have protracted spawning periods whereas the timing of peak spawning appears to be shorter in south-central Alaska (Arimitsu et al. 2008, 2012).

Forage fish and their predators tend to be tightly aggregated in the highly productive areas that occur near upwelling zones, tidal constrictions and frontal regions at the fjord sills (Fig. 3.5, Womble et al. 2014). For example, Point Adolphus is situated at the edge of the sill at the entrance to Glacier Bay with strong tidally-influenced thermal fronts joining water masses from Cross Sound, Glacier Bay and Icy Strait (Fig. 3.5, Arimitsu et al. 2007b). Although whale sightings have decreased in recent years (Neilson et al. 2015), Point Adolphus has long been an important headlands feeding area for large aggregations of humpback whales, accounting for an average of 13% of total annual whale sightings over 12 years (Chenoweth et al. 2011).

Hydroacoustic and trawl surveys at Point Adolphus found high density schools of capelin, adult herring, and walleye pollock associated with feeding humpback whales (Krieger & Wing 1986, Robards et al. 2003, Arimitsu et al. 2007b). Marine productivity hotspots, where persistent dense aggregations of marine predators and prey occur, have also been described near the sill at Muir Point in Glacier Bay (Fig. 3.5, Romano et al. 2004), in the high current velocity area in lower Glacier Bay (Renner et al. 2012, Womble et al. 2014), and near sills in Kenai Fjords (Arimitsu et al. 2010) and Columbia Bay (Fig. 3.3).

Large volumes of glacial freshwater discharge into fjord systems may make these systems more susceptible to the negative effects of ocean acidification than other marine systems in the world (Reisdorph & Mathis 2014, Meire et al. 2015). Ocean acidification is the progressive decrease in marine pH due primarily to increasing uptake of anthropogenic CO₂, however, other natural processes can also influence carbon saturation levels in the ocean.

Freshwater discharge from tidewater glaciers in Glacier Bay and in Arctic fjords have been shown to have very low total alkalinity and enhanced carbonate mineral undersaturation levels, both measures that have the potential to exacerbate anthropogenic CO₂-driven ocean acidification processes (Reisdorph & Mathis 2014, Meire et al. 2015). Ocean acidification can have varying consequences for marine organisms, but is particularly detrimental to organisms that require calcium carbonate to build shells, including pelagic gastropods important in salmon diets and crabs important to commercial fisheries (Mathis et al. 2015).

In summary, fjord scale effects of glaciers on coastal marine food webs are due to strong environmental gradients caused by the mixing of glacial freshwater with marine waters, and the influence of complex topography and bathymetry typical of glacial fjord systems (Fig. 3.4). Strong tidal currents over shallow marine sills promote mixing of nutrients and phytoplankton production where water clarity allows adequate light penetration into the water column. Depending on the degree of oceanic exposure, zooplankton are advected to and concentrated at the heads of fjords. Forage fish species like capelin spawn inshore during peak melt season and use glacier fjords as cold-water refugium. Predators and prey aggregate in frontal areas forming persistent marine productivity hot spots, often near sills and tidal constrictions that result from glacial topography. Fjords receiving large volumes of low-alkalinity glacier discharge may be the first to experience the negative effects of ocean acidification.

3.2.3 Gulf of Alaska LME

Freshwater discharge plays a key role in coastal circulation, promotes water column stability, and provides micronutrients essential for primary production in the Gulf of Alaska LME (Royer et al. 2001, Weingartner et al. 2005, Lippiatt et al. 2010). The ACC is the prominent nearshore circulation feature on the Gulf of Alaska continental shelf. Maintained by

freshwater discharge, the ACC is characterized by onshore Ekman transport that results in a predominantly coastal downwelling system (Weingartner et al. 2005). The offshore extent of the ACC varies depending on winds, sometimes confined to a narrow jet or at other times spread out over much of the shelf, and is discontinuous along its path (Stabeno et al. 2015). Relaxed downwelling in summer brings deep nitrogen-rich waters on to the shelf (Childers et al. 2005), and micronutrient-rich freshwater discharge promotes phytoplankton blooms where nitrate-rich offshore waters mix with iron-rich coastal waters (Lippiatt et al. 2010, Strom et al. 2015). The so-called high nitrogen – low chlorophyll (HNLC) conditions in offshore areas of the Gulf of Alaska are consistent with iron limitation (Strom et al. 2006), as iron is an essential micronutrient for marine phytoplankton production in the oceans (Boyd et al. 2004). Silicate, important in diatom formation, is another nutrient that can be traced to glacier runoff in the region (Lippiatt et al. 2010, Coyle et al. 2012).

Iron is supplied to the coastal Gulf of Alaska via glacial discharge and atmospheric transport. Fine glacial sediments that result from intense glacial weathering are high in iron concentration due to their volcanic origin, which is particularly bioavailable to marine primary producers due to a chlorite-dominated mineralogy (Muhs et al. 2013). Delivery of iron to the marine ecosystem occurs in several ways. Glacier-fed rivers and tidewater glaciers in the region provide iron-rich melt water to coastal areas in the summer (Fig. 3.4). While important to primary production in coastal waters, as much as 85% of melt water-derived dissolved iron and 41% of total dissolvable iron in glacial sediments is quickly exhausted within the estuarine plume (Schroth et al. 2014). Still, several studies have demonstrated the importance of meso-scale eddies in cross-shelf transport of riverine iron sources to HNLC waters in the Gulf of Alaska (Lippiatt et al. 2010, Brown et al. 2012). Wind is another important mode of iron

transport to offshore waters (Crusius et al. 2011, Muhs 2013, Ladd et al. 2015). The particle size of glacially weathered rock is suitable for long-range transport by katabatic winds that occur frequently in fall and winter, and recent work has shown that Copper River Delta glacial sediments may be a globally important source of iron to the world's oceans (Muhs et al. 2013, Muhs 2013).

At longer time scales iron enrichment to the Gulf of Alaska and North Pacific ocean has been associated with higher productivity cycles over glacial-interglacial periods in Earth's history (Davies et al. 2011, Praetorius et al. 2015). The paleorecord stored in sediment cores from the Gulf of Alaska region suggests that retreat of the Pleistocene glaciers, along with melt water pulses that caused rapid sea-level rise, coincide with periods of high diatom productivity in the North Pacific (Walinsky et al. 2009, Davies et al. 2011, Addison et al. 2012). Two abrupt deglacial warming events (+ 4 - 5°C) coincide with periods of greater nutrient utilization and high levels of diatom production in the North Pacific, with sediment $\delta^{15}\text{N}$ and microfossil abundance indicating greater denitrification and increased export productivity to the seafloor (Praetorius et al. 2015). Hypotheses for the primary productivity spikes associated with deglaciation center around ways in which iron may have been delivered to coastal and offshore areas in the Gulf of Alaska, such as 1) increasing meltwater discharge and periodic glacial lake outbursts, 2) rising sea levels, which remobilized iron and other limiting nutrients from continental shelves and estuaries, or 3) wind delivery of iron-rich glacial dust particles to offshore areas (McDonald et al. 1999, Davies et al. 2011).

The abundance of marine resources in the region has maintained Alaskan commercial and subsistence fishing communities for generations (Himes-Cornell & Hoelting 2015). Dust from glaciogenic sources provides iron that fuels marine primary production in the Gulf of Alaska

(Muhs et al. 2013). Large volumes of freshwater discharge (both precipitation and glacier runoff) drive coastal circulation (Royer & Grosch 2006, Neal et al. 2010, Hill et al. 2015). These unique connections between terrestrial and marine ecosystems create productive waters that support high levels of commercial fisheries catch, revenue, exports, employment and economic activity (Fissel et al. 2015). In 2015 the Alaska Department of Fish and Game estimated that 71 % of the total harvest (1.07 billion lbs of fish) and 66 % of the ex-vessel value (\$4.1 million) of the state's salmon fishery came from Gulf of Alaska coastal waters (i.e., southeast Alaska, Prince William Sound, Cook Inlet, and Kodiak, data available at <http://www.adfg.alaska.gov/index.cfm?adfg=CommercialByFisherySalmon.exvesselquery>, accessed Feb 24, 2016). Coastal waters also provide important rearing habitat for valuable commercial groundfish species including walleye pollock and sablefish (Brodeur & Wilson 1996, Yasumiishi et al. 2015). In this way glaciers indirectly influence human resource use and socioeconomics in the Gulf of Alaska.

Owing to freshwater discharge, high levels of marine productivity, and other factors that cause naturally low carbonate ion concentrations in the oceans, coastal regions in the Gulf of Alaska and North Pacific are already close to geochemical thresholds that will cause negative changes in the marine ecosystem in the coming decades (Mathis et al. 2015). The functioning of marine ecosystems, commercial and subsistence fisheries, economies and livelihood of coastal communities that depend on ocean resources will likely be affected. For example, red king crab yields and profits are projected to decline in the coming decades due to lower pre-recruit survival with decreased ocean pH levels (Punt et al. 2014).

In summary, at the basin scale freshwater discharge from glaciers and precipitation is a driver of coastal circulation in the Gulf of Alaska (Fig. 3.4). Glacier sediments are rich in iron

and silicate, and these nutrients are essential for marine phytoplankton production in offshore waters. Coastal topography facilitates the efficient delivery of fine glacier sediments to offshore areas by wind and eddies. Evidence from sediment cores in the Gulf of Alaska and North Pacific suggest that iron has played an important role in fueling primary productivity during glacier meltwater periods associated with past interglacials. The highly productive waters of the Gulf of Alaska support commercial fisheries which are important to local and state economies in the region. Ocean acidification due to increasing discharge of glacier melt water along with increasing anthropogenic CO₂ levels in the atmosphere may cause lower yields and profits in shellfish fisheries within decades.

3.3 Glacier change and coastal ecosystems in the future

Glacier wastage across the globe is well documented (IPCC 2014) and contemporary projections of global warming indicate warmer oceans and significant decrease in glacier volume in the 21st century and beyond (Radić & Hock 2011). Warming in Alaska is expected to increase freezing altitudes, reduce snow accumulation and cause accelerated rates of glacier thinning. More snow will fall as rain, thus earlier peak discharge and flashy hydrographs are predicted in the future (O'Neel et al. 2015). Changing glacial coverage will be a primary driver of glacier meltwater flux in the future (Hood & Scott 2008). Most of the glacier systems in Alaska are already losing mass (Larsen et al. 2015), and changes in discharge rates under a warming climate will depend on glacier volume available for melting in the future. Where glacier volume is high, melting ice will initially increase in glacier discharge into coastal areas. Diminished glacier volume will eventually lead to reduced glacier discharge into coastal areas as they transition into precipitation dominated systems.

The largest loss of glacier mass occurs in maritime regions (Larsen et al. 2007). Tidewater glacier dynamics are complex, and generally include a period of prolonged advance followed by a period of rapid retreat and dynamic instability due to low elevation relative to equilibrium line, as well as calving and submarine melting processes (Meier & Post 1987, O’Neel 2005, Larsen et al. 2007, Bartholomaus et al. 2013). Although some are in an advancing stage of the tidewater glacier cycle, most (62%) of the 50 tidewater glaciers examined within Alaska retreated between 1948 and 2012 (McNabb & Hock 2014). Alaska’s 37 remaining tidewater glaciers are in a “retracted stable” state (Post et al. 2011, McNabb & Hock 2014) because the majority of their post- Little Ice Age retreat has already occurred (Larsen et al. 2015). At the glacier-sea interface, subglacial discharge and warm seawater interact to cause subglacial melt (Bartholomaus et al. 2013). An increase in freshwater discharge into the Gulf of Alaska is predicted to increase the flow of the ACC and advect warmer water from the south to coastal areas (Royer et al. 2001). This positive feedback loop will cause greater submarine melting rates to tidewater glaciers (Bartholomaus et al. 2013) and increase instability and calving at the terminus until they reach a grounded state. The influence of these predicted changes in tidewater glaciers and meltwater discharge volume on coastal ecosystems also differs at local, meso- and basin scales (Tables 3.1 – 3.3).

At local scales the transition from tidewater to grounded glacial states has important implications for delivery of meltwater to fjord ecosystems and predator – prey dynamics (Table 3.1). Submerged freshwater flow from below tidewater glaciers and ice calving events generate local upwelling at the face of the glacier (Straneo et al. 2011), bringing krill and other zooplankton to the surface in the buoyant plume. In Kongfjorden, Svalbard, it was estimated that up to 15% of the zooplankton standing stock is removed from the water column due to osmotic

shock resulting from this process (Zajaczkowski & Legeżyńska 2001). In the absence of local upwelling and mixing from large ice calving events, krill mortality due to osmotic shock may be reduced as they are able to vertically migrate below the surface lens to more favorable habitat. In this scenario krill will no longer be brought to the surface by calving ice events, thus opportunistic feeding by surface-oriented seabird predators will be reduced as well. As glaciers diminish in size and meltwater discharge decreases, predator-prey dynamics related to turbidity in the plume will be disrupted because prey will move deeper to avoid light and predators. Kittlitz's murrelets may incur greater energetic costs if changing prey dynamics in proximity to their nesting habitat requires them to fly farther distances to feed and provision their chicks (Agness et al. 2008). Furthermore, grounded glaciers will not provide the ice haul-out substrate for pupping harbor seals, causing greater exposure to predators. Initially glacier tourism may boost local and state economies and brings greater climate change awareness to the public, however, as tidewater glaciers recede and glacier size diminishes, glacier-driven tourism will be reduced.

At fjord scales the initial increase in glacier discharge to marine ecosystems has a strong effect on the thermohaline structure and other physical aspects of coastal habitat (Table 3.2). Changes in the temperature, salinity, nutrients and turbidity may alter phytoplankton dynamics in the fjords. For example, nutrient availability may become more important than light availability if less glacial sediment is released in runoff, and lower silicate concentrations resulting from reduced runoff may suppress diatom production after the spring bloom (Sieracki et al. 1993). However, as glaciers recede, glacier discharge warms before entering coastal waters and also contains greater concentrations of dissolved inorganic nitrogen due to the influence of early successional plants (Hood & Scott 2008). This could result in changes in nutrient concentrations

that benefit primary producers in the fjords. Higher trophic levels, however, may experience negative effects of ocean acidification with increasing glacier discharge. Low alkalinity glacier discharge reduces the buffering capacity of the ocean to regulate pH, and increased corrosivity and low aragonite saturation levels may have negative effects on shell-bearing organisms (e.g., crabs and pelagic snails) and corals (Reisdorph & Mathis 2014, Mathis et al. 2015). As warming continues and cold glacier discharge diminishes, the fjords may no longer serve as cold-water refugia for species like capelin that require colder temperatures (Rose 2005, Arimitsu et al. 2008). As tidewater glaciers diminish in size and glacier-driven tourism decreases there may be fewer cruise ships and tour vessel traffic in the fjords, and this could reduce vessel-related disturbance to seabirds and marine mammals (Agness et al. 2008, Harris et al. 2012).

At the basin scale changes in freshwater flux to the ocean will have a greater influence on the marine ecosystem than changes in tidewater glacier volume (Table 3.3). An increase in freshwater discharge in coastal areas of the GOA is predicted to increase ocean salinity and temperature because greater cross-shelf density and sea-level pressure gradients will cause greater alongshore flow in the ACC and advect warm and saline water from the south (Royer et al. 2001). Iron trapped in more frequent eddies (Royer et al. 2001) will fuel marine phytoplankton in offshore areas (Crawford et al. 2007). Marine communities may reorganize in response to large-scale shifts in temperature and trophic control (bottom up or top down), as has been observed in the Gulf of Alaska previously (Anderson & Piatt 1999, Hare & Mantua 2000, Litzow & Ciannelli 2007). Rates of sea level change, which may affect coastal communities, will vary by coastal region depending on the effects of ocean volume (greater in south-central AK) compared to the effects of glacier rebound in response to ice sheets on land (greater in southeast AK) (Shugar et al. 2014). With increased atmospheric CO₂ levels and increased freshwater

discharge influencing ocean pH (Mathis et al. 2015), the effects of ocean acidification on shellfish fisheries in Alaska are predicted to lower fisheries yields and profits within decades (Punt et al. 2014). Additionally, as glaciers diminish in size and become less accessible the tourism draw to the state may become less diversified and potentially less profitable.

Future research addressing gaps in our understanding of the influence of glaciers on marine ecosystems will help coastal resource managers make informed decisions. At local scales, further work comparing plume dynamics between glacial and non-glacial stream systems and also to better understand the response of benthic communities to glacier runoff will fill gaps in our understanding of how marine communities will respond to changing glacier coverage. A greater understanding of fjord-scale processes, for example the extent of benthic-pelagic coupling in marine ecosystems, will inform coastal resource managers. Further, fjords receiving glacier runoff may be the first to experience the effects of ocean acidification and these coastal ecosystems may provide a greater understanding of how marine food webs respond to ocean acidification. Finally, future research should focus on basin-scale linkages between iron and food webs, as well as sustainable ecosystem-based fisheries management.

3.4 Conclusion

The earth's ability to store ice and release liquid water is one of its most important features for life on the planet. The examples presented here show that glaciers have and will continue to shape terrestrial-marine connections in the North Pacific. Our contemporary understanding of glacier influence on marine ecosystems is underscored by several factors including 1) a complex topography, bathymetry and fjord geometry left behind by receding glaciers, 2) the frontal zones where fresh and marine water come together that tend to form dense aggregations of prey and predators, 3) the biogeochemical role of iron in glacial dust and

intensely weathered glacial riverine sediments that promote diatom blooms and drive bottom up processes in higher trophic level organisms.

In the near term glacier volume loss will increase glacier melt water discharge into coastal marine ecosystems and glacial fjords may serve as a cold water refugium for some species intolerant of the impending warm ocean conditions. Plasticity in behavior of higher trophic level species to changes in the marine environment may attenuate the effects of warming and ice loss, for example fish may compensate for warmer temperatures through shifts in distribution (Rose 2005, Mueter & Litzow 2008) and seabirds may adjust foraging behavior and energetic budgets to buffer the impact of changing prey fields (Grémillet et al. 2012). Some species may take refuge in cooler water temperatures at depth; for example, it is thought that subtidal spawning in capelin was an evolutionary adaptation to ice conditions in the Atlantic during the last glacial maximum (Stergiou 1989). On the other hand, pagophylic species that have evolved with the cryosphere and are associated with ice or cool temperatures as a basic part of their life history, like the Kittlitz's murrelet, may be most susceptible to extinction in a warming climate.

Cycles of the cryosphere will continue as they have for eons but will be forever altered from a truly natural state in the age of the Anthropocene (Waters et al. 2016). The rate of atmospheric carbon increase due to anthropogenic activities over relatively short time scales is unprecedented and may result in an abrupt transition to an unknown climate state. Melting ice sheets and glaciers, rising sea level, and iron flux to the oceans will be driving agents of change in marine phytoplankton regimes and the food webs they sustain.

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Table 3.1. Local-scale (< 10 km) influence of changing glacier runoff volume and diminishing tidewater glaciers on coastal marine ecosystems in the Gulf of Alaska.

Process	Habitat	Biology	Humans
Initial increase in glacier discharge due to melting	Low temperature and salinity, high stratification, high turbidity, high nutrients (both from riverine sources and low demand by phytoplankton)	Light-limited phytoplankton, low-density, shallow prey provides foraging opportunities for nesting birds, availability of ice haul out substrate for pupping seals	Glacier tourism boosts local and state economies and brings greater climate change awareness to the public
Tidewater glaciers recede and eliminate ice calving processes and floating ice bergs	Submerged discharge source transitions to warmer riverine-like surface discharge, reduction of plume foraging habitat, reduction of ice-related processes	Reduced zooplankton mortality from osmotic shock Absence of calving processes reduce opportunistic feeding by surface-feeding marine birds Reduction of haul-out substrate for pupping harbor seals	Glacier-driven tourism is reduced.
Diminished glacier discharge, smaller alpine glacier mass loss is dominated by surface melt in warming conditions	Transition to precipitation dominated system - flashy hydrograph, earlier peak in freshwater discharge	Change in predator-prey dynamics: prey move to deeper water to avoid light and predators Increased energetic costs for nesting and feeding Kittlitz's murrelets Changes in phenology	Glacier-driven tourism is reduced.

Table 3.2. Meso-scale (< 100 km) influence of changing glacier runoff volume and diminishing tidewater glaciers on coastal marine ecosystems in the Gulf of Alaska.

Process	Habitat	Biology	Humans
Initial increase in glacier discharge due to melting	Maintenance of strong freshwater to marine environmental gradients in fjords during the melt season	<p>Silicate fuels prolonged diatom blooms where glacial sediments settle out</p> <p>Marine communities are structured along glacier runoff gradients – cool fresh to warm saline conditions</p> <p>Low alkalinity glacier discharge reduces the buffering capacity of the ocean to regulate pH, increased corrosivity has negative effects on shell bearing organisms and corals</p>	
Tidewater glaciers recede and eliminate ice calving processes and floating ice bergs	Glacier river runoff may warm before entering coastal waters and contain greater concentrations of dissolved inorganic nitrogen due to nitrogen-fixing early successional plants	<p>Change in phytoplankton dynamics: nutrient rather than light availability becomes key structuring feature, less silicate from runoff may suppress diatom production after the spring bloom.</p> <p>Lower incidence of marine mammal injuries and mortalities from ship strikes</p>	Reduced tourism from cruiseships and tourboats
Diminished glacier discharge, smaller alpine glacier mass loss is dominated by surface melt in warming conditions	More homogenous marine environment, warmer more saline conditions Fjords will no longer be cold-water refugia for organisms	<p>Reorganization of zooplankton, fish, seabird and marine mammal communities in fjords</p> <p>Warm water species thrive, cold water species disappear</p>	Reduced tourism from cruiseships and tourboats

Table 3.3. Basin-scale (1000s km) influence of changing glacier runoff volume and diminishing tidewater glaciers on coastal marine ecosystems in the Gulf of Alaska.

Process	Habitat	Biology	Humans
Initial increase in glacier discharge due to melting	Increased salinity, temperature (due to advection of warmer water from the south), greater windstress and precipitation rates, greater cross-shelf density and pressure gradients, greater alongshore flow in the ACC (Royer et al 2001)	Iron exports to offshore areas fuel primary productivity and higher trophic level organisms Marine community reorganization	Rates of sea level rise along the coast will vary by coastal region based on the effects of ocean volume vs. glacier rebound in response to ice sheets on land; south-central AK coastal communities are at greater risk of inundation than southeast AK Effects of ocean acidification may lower profits and yields of shellfish fisheries
Tidewater glaciers recede and eliminate ice calving processes and floating ice bergs	Exposed glacier sediments continue to fuel wind driven iron exports to the ocean for millennia		Tourism draw to the state is less diversified and potentially less profitable
Diminished glacier discharge, smaller alpine glacier mass loss is dominated by surface melt in warming conditions	Increase salinity, lower cross-shelf density, lower alongshore flow	Iron exports to the ocean are still possible through wind, eddy and sea level rise at the coastal margin	

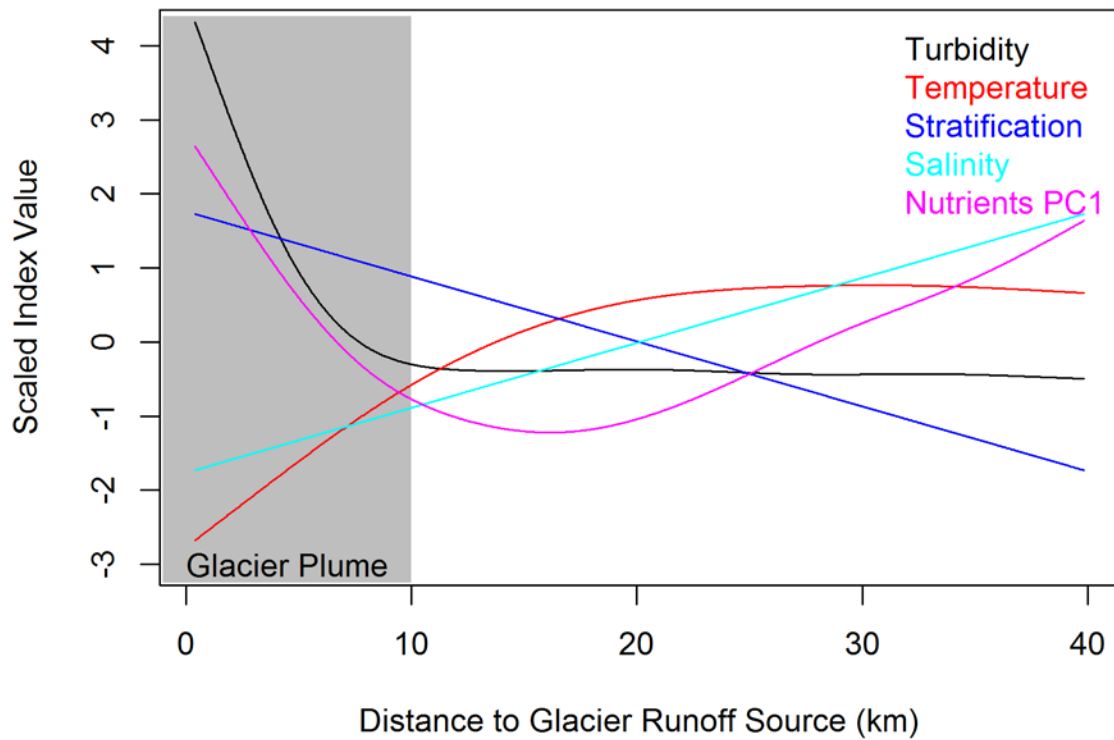


Fig. 3.1. Relationship between physical and nutrient indices relative to glacier runoff sources in Glacier Bay, Alaska during June-July 2004. Colored lines represent non-linear (black, red, pink: general additive model) or linear (blue, light blue: ordinary least square regression) predictions of near-surface indices of turbidity, temperature, salinity, stratification ($\Delta\sigma_t$) and nutrient variability (first principal component, PC, of nitrate, nitrite, ammonium, phosphate and silicate) relative to distance to the nearest glacier runoff source. Predictions for all indices were scaled to a mean of 0 and standard deviation of 1 to facilitate plotting on a common scale. The near-surface waters in the glacier plume waters (grey shaded region) are characterized by strong gradients in turbidity, temperature, and nutrients.

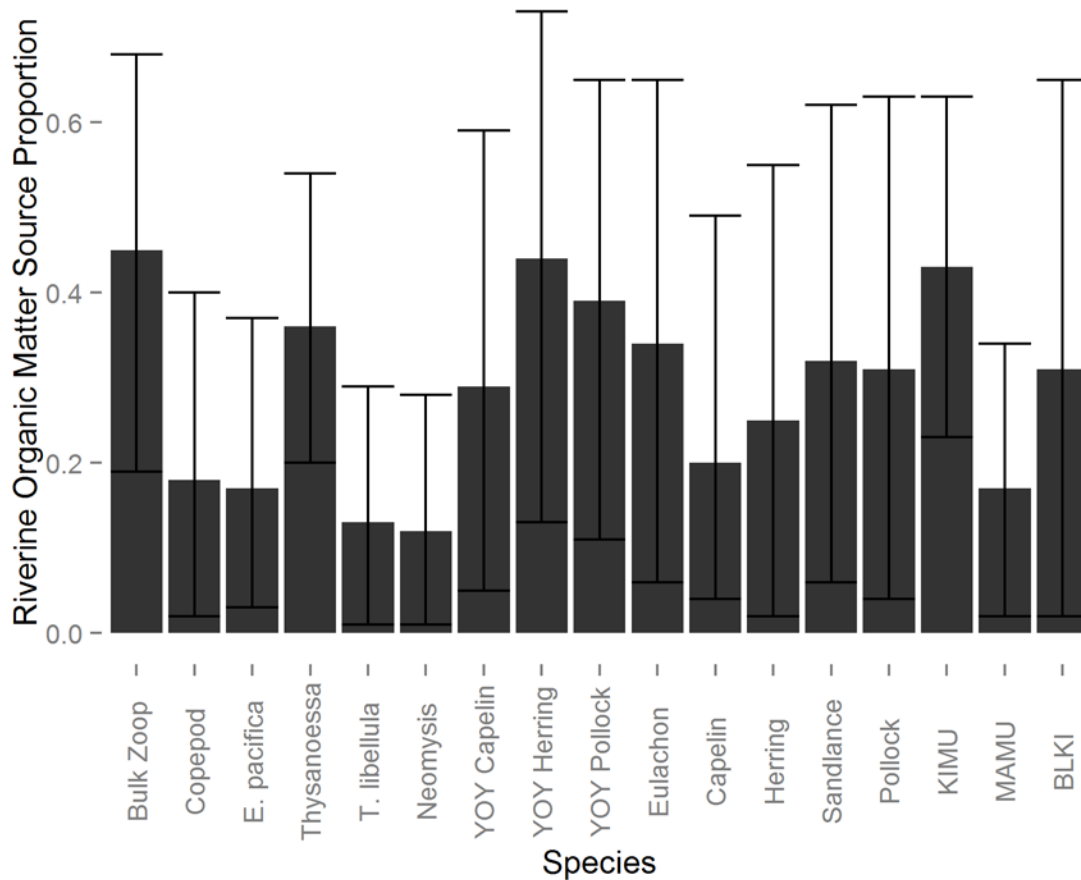


Fig. 3.2. Median values of riverine organic matter source proportion for species sampled near glacier river plumes (see chapter 2). Error bars represent 95% credible intervals of the posterior distributions. Species are arranged in order of increasing trophic level from bulk zooplankton (zoop), calanoid copepods, krill (*Euphausia pacifica* and *Thysanoessa* spp.), amphipods (*Themisto libellula*), mysids (*Neomysis rayii*), young of the year (YOY) fish (capelin, herring pollock), age 1+ fish (eulachon, capelin, herring and sandlance), and seabirds (Kittlitz's murrelet, KIMU; marbled murrelet, MAMU; black-legged kittiwake, BLKI).

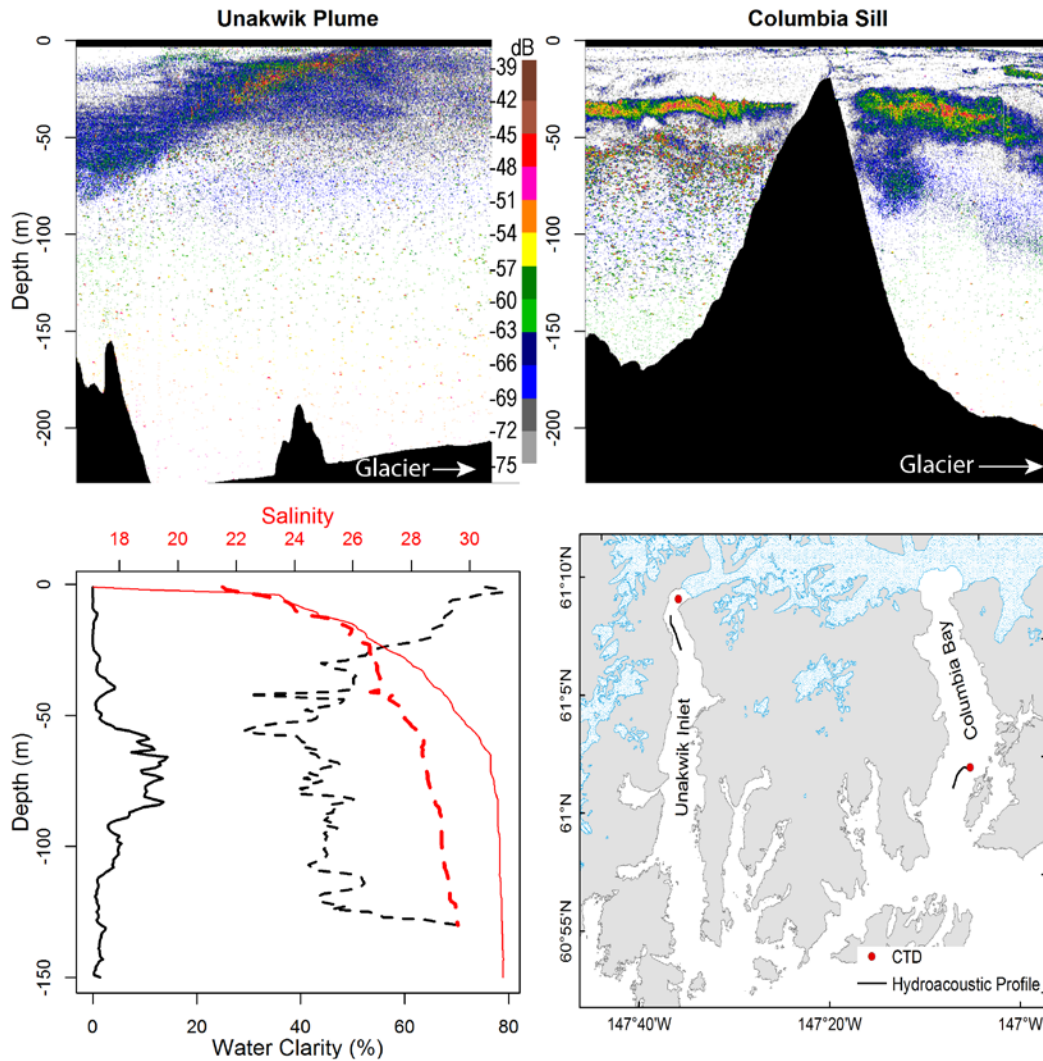


Fig. 3.3. Hydroacoustic echograms showing representative examples of 120 kHz backscatter (color, dB, seafloor shown in black) relative to depth (y-axis, m) along a 3 km long transect segment moving towards tidewater glaciers. Top left (local scale): Prey layer in the glacier plume waters of Unakwik Inlet, July 25, 2015. Backscatter was composted of a layer of krill and dispersed planktivorous pollock, capelin, herring and eulachon that became shallower near the glacier. Top right (fjord scale): Columbia Bay, July 23, 2015. Backscatter was composed of krill and adult pollock concentrated near the sill. Bottom left: Salinity (red) and beam transmission (black) profiles taken in Unakwik (solid lines) and Columbia Bay (dashed lines) shows low salinity surface layers in both fjords, and differences in water clarity between plume waters (Unakwik) and near a sill (Columbia). Bottom right: Map of CTD and transect locations, glaciers are shown in blue.

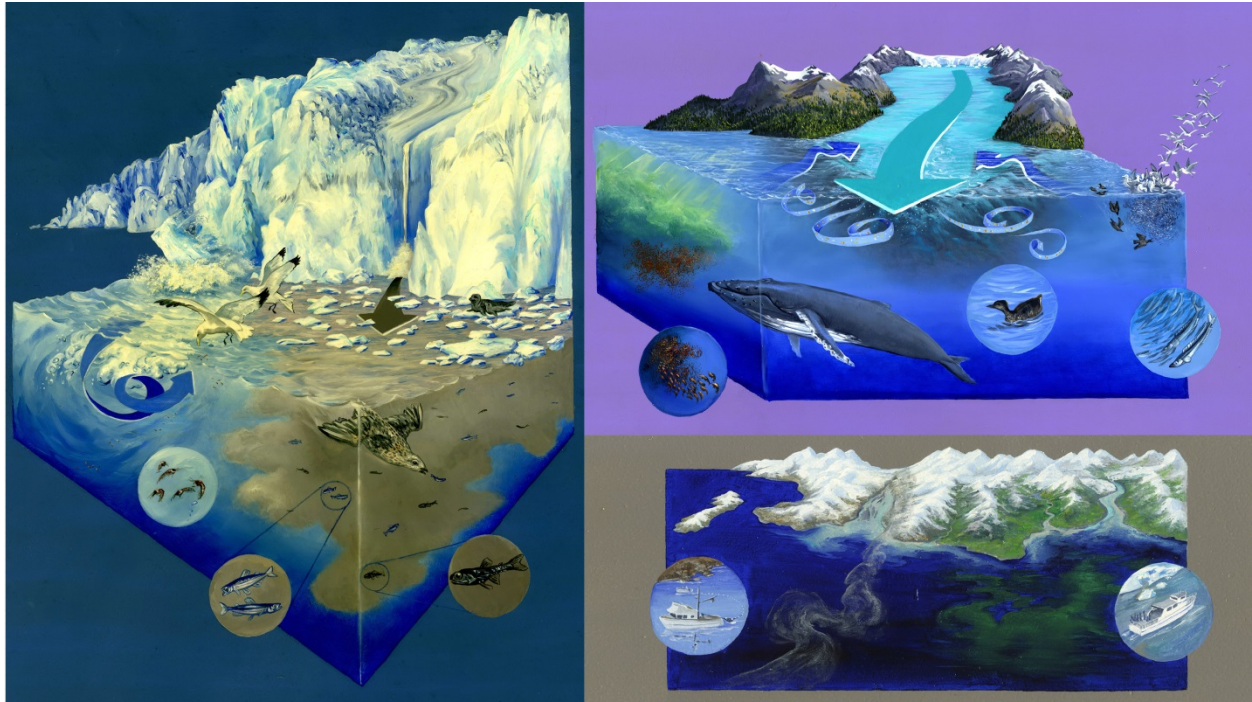


Fig. 3.4 Scale dependent influence of tidewater glaciers on coastal marine food webs. Left: Local scale (< 10 km). Breeding seabirds feed on dispersed krill and forage fish in turbid plume waters. Calving ice makes prey available to surface-feeding gulls and provides habitat for pupping seals. Top right: Meso-scale (< 100 km). Hotspots of marine productivity and dense predator-prey aggregations occur where there is mixing of fresh and marine waters. Large tides, constricted passages and shallow sills that mark previous glacier termini replenish nutrients for phytoplankton growth where there is more light in the water column because the glacier silt settles out. Bottom right: Basin scale (1000s km). Seasonal changes in discharge volume and wind storms influence circulation and induce iron exports to sea via riverine, eddy and aeolian dust transport. Iron promotes offshore phytoplankton blooms that fuel higher trophic levels, such as commercially important fish and other wildlife. Glaciers are an important draw for a growing tourism industry in coastal Alaska, and the earth's disappearing cryosphere is increasingly a visible and irrefutable indicator of climate change. Artwork credit: Bruce Nelson.

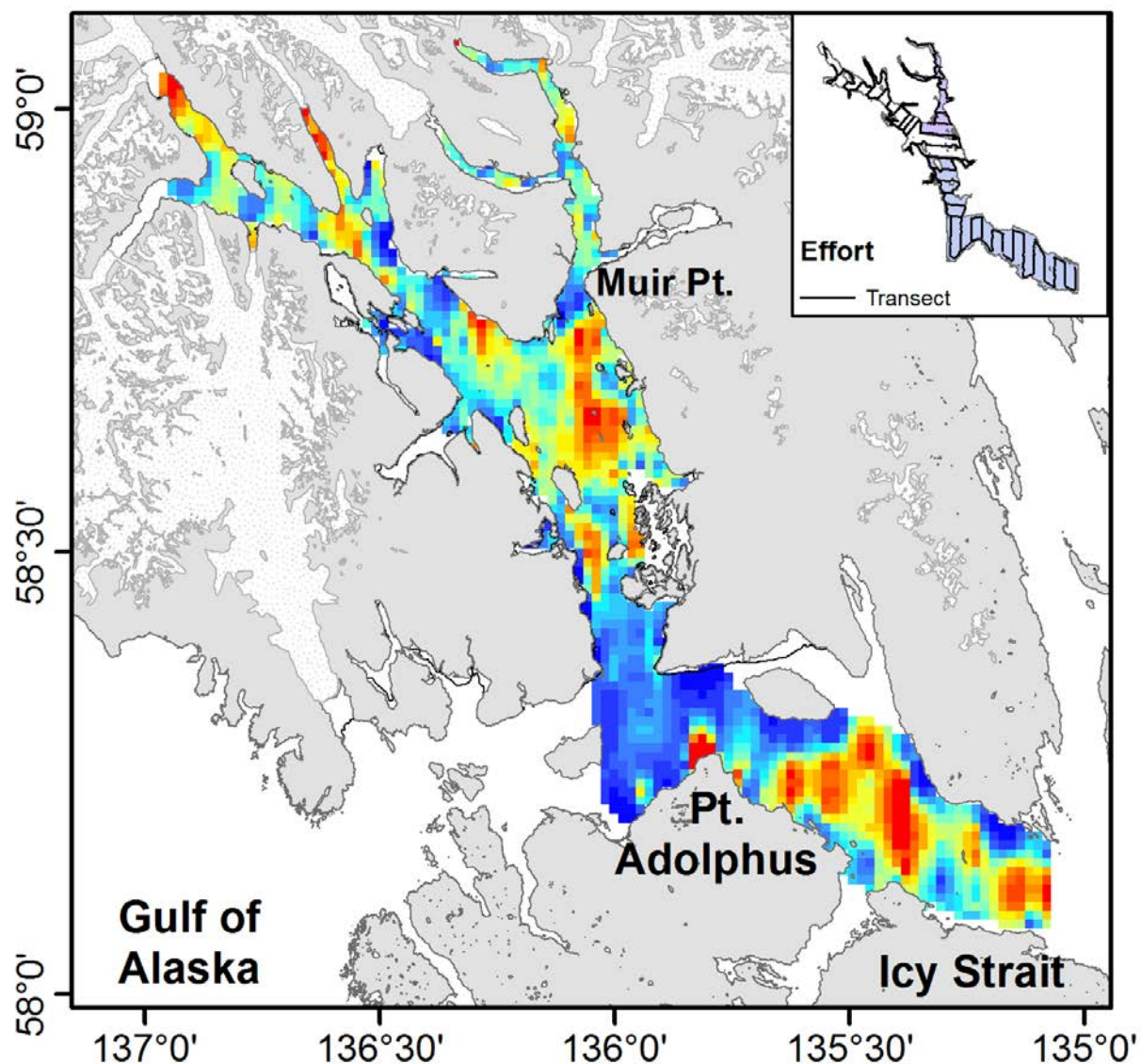


Fig. 3.5. Horizontal distribution of 120 kHz acoustic backscatter (nautical area scattering coefficient, NASC anomaly, warmer colors indicate above average and cooler colors represent below average mean backscatter) showing the relative distribution of biomass in the upper 50 m of the water column in Glacier Bay and Icy Strait, Alaska in June 1999. See appendix 3.7.1 for methods.

3.7 Appendices

Appendix 3.7.1 Supplemental information

3.7.1.1 Hydroacoustic data collection and interpolation methods

Hydroacoustic data, often used to describe density and depth distribution of fish and other nekton biomass in the water column, have been summarized for several fjord systems (Robards et al. 2003, Arimitsu et al. 2012, Womble et al. 2014). To augment past work and graphically illustrate representative examples of the vertical distribution of prey in tidewater glacier fjords I used hydroacoustic – trawl datasets from the Meares Glacier Plume in Unakwik Inlet, and from the sill that separates the inner and outer glacial fjord in Columbia Bay, Prince William Sound (SIMRAD 120 kHz split beam echosounder deployed in July 2015) and Glacier Bay (Biosonics 120 kHz single beam echosounder deployed in June 1999, see Robards et al. 2003 for survey details).

Both echosounder systems were calibrated in the field by suspending a tungsten-carbide sphere of known target strength below the echosounder according to Foote et al. (1987). Prince William Sound data were preprocessed in Echoview v.5.4 (Myriax, 2013). Passive noise and background noise was removed (De Robertis & Higginbottom 2007, Parker-Stetter et al. 2009). Echo returns in the near field above 5 m and below the seafloor were removed.

In Glacier Bay, hydroacoustic backscatter (NASC, $\text{m}^2 \text{ n mile}^{-2}$) data were vertically integrated in the layer between 5 and 50 m depth, where more than half of the measured water column biomass occurred (Robards et al. 2003), and horizontally binned at 250 m intervals. Due to the irregular shaped coastline that impede Euclidean distance calculations through the water, I interpolated data in the east, west and lower bay/Icy Strait subregions separately (Fig. 3.2 inset) using the krig.bayes routine in the ‘geoR’ package (Diggle & Ribeiro Jr. 2007, Ribeiro Jr. &


Diggle 2015) with R statistical software (R Core Development Team, 2014). Predictions of log-transformed and centered 120 kHz acoustic backscatter were made using a grid spacing of 0.01 degrees (1 km resolution) assuming second order stationarity in the mean and a Gaussian likelihood for mean backscatter with prior distribution $N(0, 1000)$. The sill (σ^2) was given an improper prior distribution proportional to $1/\sigma^2$ where $\sigma^2 > 0$, the range (ϕ) had an exponential prior with mean = 0.01, and the nugget (τ^2) was parameterized according to the convention used in ‘geoR’ as omega ($\omega = \tau^2/\sigma^2$), which was given a uniform prior distribution between 0.7 and 0.8 because this parameterization best facilitated model convergence. The posterior distribution was sampled using Markov chain Monte Carlo (MCMC) with a chain length of 1000, 200 sample burn in and thinning rate of 2 out of 3 iterations. After examining trace plots to ensure appropriate convergence of model parameters for each subregion, point predictions were back-transformed, rasterized and plotted on a common scale across all subregions.

3.7.1.2 References






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Appendix 3.7.2 Permission to use conceptual graphic



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Conclusion

In this work I examined the physical and organic matter (OM) resource subsidy pathways from glacier runoff to marine food webs, and also synthesized information on the scale-dependent influence of glaciers on marine ecosystems. Glacial runoff provides large volumes of freshwater to fjord systems in the Gulf of Alaska (Larsen et al. 2015), and modifies marine habitat gradients that structure dynamics of phytoplankton and higher trophic levels. It also provides a pulse of modern terrigenous and ancient glacier-derived organic carbon to coastal food webs (Hood et al. 2009). In the light and phytoplankton-limited marine food web, stable isotope data suggest moderate use of allochthonous subsidies by copepods, krill, forage fish and seabirds. Furthermore, the glacial-marine food web in Prince William Sound was isotopically distinct from the more oceanic food web in the Western Aleutians. This work contributed to a greater understanding of glacier influence at small to large spatial and temporal scales.

In chapter one I used generalized additive models and geostatistics to identify the range of influence of glacier runoff in fjords of varying estuarine and topographic complexity. I also modeled the responses of chlorophyll a concentration, copepod biomass, fish and seabird abundance to physical, nutrient and biotic predictor variables. Physical and nutrient signatures of glacial runoff extended 10-20 km into coastal fjords. Glacially modified physical gradients and among-fjord differences explained 66% of the variation in phytoplankton abundance, which is a driver of ecosystem structure at higher trophic levels. Copepod, euphausiid, fish and seabird distribution and abundance were also related to environmental gradients that could be traced to glacial freshwater input. Seabird density was predicted by prey availability and silica concentrations, which may indicate upwelling areas where this nutrient is in excess. Similarities in ecosystem structure among fjords were due to influx of cold, fresh, sediment and nutrient

laden water, while differences were due to fjord topography and the relative importance of estuarine vs. ocean influences.

In order to demonstrate connectivity between terrestrial and marine ecosystems, in chapter two I used stable ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^2\text{H}$) and radiogenic ($\Delta^{14}\text{C}$) isotopes to estimate the proportional contribution of riverine OM to marine food webs. I sampled dissolved organic matter (DOM), dissolved inorganic matter (DIC) and particulate organic matter (POM), mussels, plankton, fish and seabirds near tidewater glaciers during the peak melt in summer. Based on $\delta^2\text{H}$ values of water at 10 m depth, mixing and infiltration of glacial runoff extended roughly 45 km from Columbia Glacier, the largest tidewater glacier in Alaska. I developed a Bayesian isotope mixing model that simultaneously integrated $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ abundance from three discernable sources and 14 species groups representing lower, middle and upper trophic levels. Posterior mean point estimates of the glacial freshwater source contribution to coastal food web components ranged from 12 - 45 %, and differences among species were likely due to variation in life history and foraging habits. For example, Kittlitz's murrelets, which are strongly associated with turbid glacier plumes, had a greater proportion of riverine OM use compared to marbled murrelets, which are more associated with coastal waters outside of glacier plumes. Similarly, different krill species (*Euphausia pacifica* vs. *Thysanoessa* spp.) were different in their riverine OM use, which was consistent with their offshore vs. neritic habitat use, respectively. However, radiocarbon data indicate ancient carbon derived from glacial ecosystems does not subsidize coastal marine food webs as biota from pelagic and benthic habitats were composed of 92 - 99% modern carbon, which was similar to biota at a reference oceanic site without glacial runoff.

Last, I synthesized information on the influence of Alaska's coastal glaciers on marine food webs at varying spatial and temporal scales. Glacial melt water provides a seasonal pulse of cold, fresh, nutrient and sediment-laden water into coastal areas of Alaska. At local scales (< 10 km) phytoplankton production is limited by shallow light penetration beyond the surface lens of glacial runoff, however, rich zooplankton and forage fish communities still occur in these plumes. Mesopelagic species occur close to the surface during daytime owing to low light availability in the shallow turbid layer. Light reduction in turbid waters and noisy ice acoustics may also limit visual and auditory cues for subsurface marine predators (Pettit et al. 2015), while osmotic shock and upwelling of near-surface prey near calving glaciers can benefit surface-oriented seabird predators (Zajackowski & Legeżyńska 2001, Lydersen et al. 2014). At fjord-scales (10 - 100s km) glacial freshwater delivers nutrients and imparts optimum stratification necessary for prolonged phytoplankton production observed in some fjord systems (Etherington et al. 2007, chapter 1). The crossroads of estuarine dynamics, oceanic influences and tidal interactions with complex fjord geometry creates productive waters for pelagic communities. At basin-scales (100 - 1000s km), freshwater influx is a driver of the Alaska Coastal Current (ACC), which can be traced from the Gulf of Alaska coast into the Bering Sea (Woodgate & Aagaard 2005). Large-scale primary productivity downstream of glaciers and in offshore areas of the Gulf is enhanced by iron-rich runoff into coastal areas (Coyle et al. 2012, Schroth et al. 2014), through cross-shelf transport of this runoff via ocean eddies (Brown et al. 2010), and by dust storms that carry iron-rich glacial silt into marine waters during the fall and winter (Crusius et al. 2011, Muhs et al. 2013).

This contemporary understanding of glacial influence on marine ecosystems is underscored by the paleorecord stored in sediment cores over geologic time scales. Iron

enrichment is hypothesized to be a mechanistic driver of high productivity pulses in relation to melt water influx and sea level rise over abrupt deglacial warming periods in the past 17000 years (de Vernal & Pedersen 1997, Davies et al. 2011). Thus glacial influence has been an important influence on the North Pacific marine ecosystem for eons.

We anticipate continued changes in the volume and magnitude of glacial runoff will affect coastal marine food webs in the future. The nature of the effects on the biology of coastal ecosystems will depend on the ability of species to tolerate and adapt to changing conditions. Given the predicted impact of global warming on glacier thinning and retreat in the GOA, this work facilitates a greater understanding of how projected changes in freshwater discharge from glaciers will directly impact the biophysical properties of coastal marine ecosystems.

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